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Change in Editorship

For over 15 years, James K. Lowry has been Editor of the *Records of the Australian Museum*. During this time, he was responsible for the scientific content of over 45 issues of the *Records*, 24 *Supplements* and 14 *Technical Reports*. Although he became Editor in 1982, the first issue of the *Records* to bear his name as Editor was 35(1), published in June 1983. This issue was the first in the then new (and current) format of A4, two columns, that Jim Lowry instituted, and prior to that change in format, the Editor was not identified in the individual issues. Coincident with this change in format, he established the *Supplement* series of the *Records* for larger contributions. As Editor, Jim's style was to work closely with authors to rectify shortcomings resulting in the best possible published paper, rather than to simply reject papers that were basically sound but deficient. This approach provided benefits to both the author and the journal. During his time as Editor, Jim not only brought the format of the *Records* up to date, introduced many changes in production that took advantage of technological advances, and increased the profile of the journal, but also solicited and published very high quality papers by researchers of international standard, particularly on Crustacea. In sum, while keeping to the goal of publishing papers within the research interests of the Australian Museum (Anthropology, Geology and Zoology), Jim made the journal more outward-looking and increased its quality in nearly every sense. It is to Jim's special credit that he maintained an active research program and published extensively on amphipod systematics during his term as Editor.

Jim Lowry now returns to the full-time job of Principal Research Scientist and has handed on to the Editorial Committee a publication series of high international standing in very good shape (certainly much better shape than when he took it on). He goes with the thanks and appreciation of everyone at the Australian Museum, and many in the wider scientific community.

A reorganisation of the arrangements for Australian Museum Scientific Publications means that no one person has to try to fill Jim Lowry's shoes. The Editorial Committee, headed by a Chair, is now responsible for scientific content. The Production Editor has expanded responsibilities and is now Editor. This new editorial team hopes to meet the high standards set by Jim during his long tenure, and will continue to strive to produce high-quality publications within the research interests of the Australian Museum.

It is also appropriate to acknowledge the many contributions of William B Rudman, who often served as Acting Editor during Jim Lowry's tenure. Bill Rudman recently stepped down from the Editorial Committee after 12 years. The Editorial Committee thanks Bill for his exemplary service.

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Chair, Editorial Committee

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Editor, Scientific Publications

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Morphological and Ecological Disparity in Naraoiids (Arthropoda) from the Early Cambrian Chengjiang Fauna, China

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ABSTRACT. *Misszhouia longicaudata* (Zhang & Hou) from the Chengjiang lagerstätte is separated from *Naraoia* Walcott by its antennular orientation, its smaller cephalic caeca and gut, lanceolate distal exopod lobe, and partial fusion of the exopod and first endopodal podomere. *Naraoia spinosa* Zhang & Hou (also from Chengjiang) shares derived characters with the type species, *N. compacta*. Deposit feeding is suggested for *Naraoia spinosa* by both morphology and preservational circumstances. New material shows previously unknown features in *Misszhouia longicaudata*, including frontal organs anterior to a sclerotised lobe of the hypostomal complex, the position of the mouth opening, details of antennule and biramous limb attachments, morphology of the sternites and limb rami, and the structure of the ventral cuticle in the cephalon and pleural areas.

CHEN, JUN-YUAN, GREGORY D. EDGECOMBE & LARS RAMSKÖLD, 1997. Morphological and ecological disparity in naraoiids (Arthropoda) from the Early Cambrian Chengjiang fauna, China. *Records of the Australian Museum* 49(1): 1–24.

The systematic status of *Naraoia* Walcott, 1912, and several allied non-mineralised arthropods has most recently been reviewed by Fortey & Theron (1994). These workers provided evidence that Naraoiidae Walcott, 1912, could be defined as a monophyletic group that unites the Lower-Middle Cambrian *Naraoia*, the Lower Cambrian *Liwia* Dzik & Lendzion, 1988, the Ordovician *Tariccoia* Hammann *et al.*, 1990, and the Upper Ordovician *Soomaspis* Fortey & Theron, 1994. Among a range of Early Palaeozoic Arachnata that are known from exceptionally-preserved faunas, naraoiids are of particular significance because they have been regarded as a possible sister or stem-group to trilobites (Fortey & Theron, 1994; Shu *et al.*, 1995).

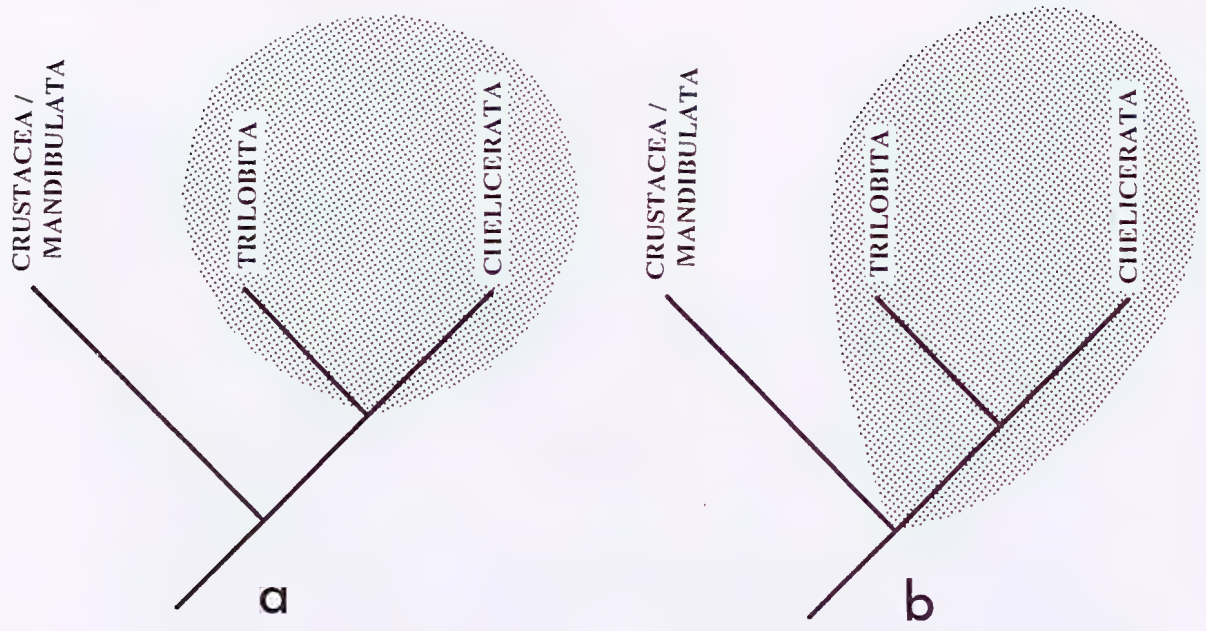

Fig. 1. Cladograms contrasting phylogenetic definitions of Arachnata. a, Node-based definition (Lauterbach, 1980). b, Stem-based definition (endorsed here).

A wealth of information on morphology and ecology of naraoiids is provided by abundant specimens from the Chengjiang fauna (Early Cambrian) of Yunnan Province, China. Zhang & Hou (1985) diagnosed the two Chengjiang naraoiids as species of *Naraoia*. The objectives of the present work are to demonstrate the breadth of anatomical and ecological variation in *Naraoia* as so defined, consider phylogenetic relationships between species, and revise the classification to reflect these relationships. We erect *Misszhouia* n.gen. for *N. longicaudata*.

Specimens illustrated in this work are housed in the Early Life Research Centre, Nanjing Institute of Geology and Palaeontology, Academia Sinica (prefixed ELRC). Material originates from the Yu'anshan Member of the Heilinpu (previously Qiongzhusi) Formation at Maotian Hill (Maotian'shan), the classic locality for the Chengjiang fauna. The *Eoredlichia/Wutingaspis* Zone, to which the Chengjiang fauna is assigned, has recently been assigned an early Botoman age (Landing, 1994; Zhuravlev, 1995), but biostratigraphic work by the senior author supports an earlier (late Atdabanian) dating. Quarries at Maotian Hill are numbered following the scheme used by Chen *et al.* (1995: 4–5).

Systematic Palaeontology

Arthropoda Siebold & Stannius, 1845

Arachnata Lauterbach, 1973

We employ the taxonomic name Arachnata with an explicit phylogenetic definition (see de Quieroz & Gauthier, 1990, 1994, for elaboration of this concept). Arachnata is that monophyletic group composed of Chelicerata and all taxa more closely related to it than to Crustacea. Lauterbach's concept of Arachnata was "node-based" in the terminology of de Quieroz & Gauthier (i.e., a clade stemming from the most recent common ancestor of Trilobita and Chelicerata) (Fig. 1a). We have adopted a "stem-based" approach (Fig. 1b) in order to also accommodate extinct taxa branching from the stem lineage of Arachnata sensu Lauterbach (1973, 1980). With this definition, Arachnata will remain a stable, monophyletic entity regardless of new discoveries of stem group taxa.

Naraoiidae Walcott, 1912

Misszhouia n.gen.

Etymology. In honour of Miss Zhou Gui-qing, for her skilled preparation of Chengjiang fossils.

Type species. *Naraoia longicaudata* Zhang & Hou, 1985.

Diagnosis. A naraoiid with antennule directed anterolaterally, proximal part not strongly deflected outwards; four pairs of relatively small digestive caeca in cephalon, without ramifying anterior diverticula; trunk a single tergite, lacking articulations (shared with *Naraoia*); gut of relatively small diameter; exopod "fan" with large surface area composed of long lamellar setae; exopod attached along entire length of basis and at least proximal part of first podomere of endopod; exopod shaft

gently tapering distally; distal lobe of exopod lanceolate, not substantially expanded; endopod composed of seven podomeres including terminal claw.

Hypostome and frontal organs. Homologies between naraoiid and trilobite hypostomes appear complex, and some discussion is required in order to use a meaningful descriptive terminology for *Misszhouia*. The structure identified by Zhang & Hou (1985) as the hypostome of *M. longicaudata* is described here as the "ovate lobe of the hypostomal complex" (Figs 2c, 3a, 4). This ventrally convex lobe is a moderately large sternite (less than 30 percent the length of the cephalon). Its margins are not strongly defined, indicating weaker sclerotisation than that of the tergites. It is longitudinally ovate, with maximum width posterior to midlength.

Anterior to the ovate lobe of the hypostomal complex are three ventrally-bulging organs, here called frontal organs, of which the medial of the three is set forward of the other two (Figs 2c,d, 3, 4). The medial frontal organ is elongate and teardrop-shaped, the lateral pair more or less ovate. All three are preserved protruding strongly ventrally with an anteroventral slope making their anterior edge vertical or even slightly protruding in front of the cuticle at its base. The frontal organs are set upon a low relief, boomerang-shaped platform that appears to represent a weakly sclerotised sternite. Some specimens show the frontal organs and ovate lobe to be surrounded and joined by a thin sheet of tissue (arthrodial membrane or ventral cuticle) that extends out to the bases of the antennules (see below). The frontal organs and ovate lobe are thus conjoined as a structural complex that may include two lightly sclerotised sternites. If the attachment site of the antennules is to be regarded as a homologous landmark between naraoiids and trilobites, it is plausible to regard the hypostomal region of *Misszhouia* as including the whole complex—frontal organ sternite, the ovate lobe, and the intervening field of arthrodial membrane—and extending out to the antennular bases. This may, however, be a dubious assumption, given Müller & Walossek's (1987: 47) observations on the lability of antennular position within Crustacea. The lateral and posterior margins of the hypostomal complex are poorly defined (Fig. 2b–d); it is not certain that the shield-shaped impression seen in some specimens (Fig. 5b) is an accurate outline of the hypostomal complex.

Whittington (1977) noted that the hypostome of *Naraoia* was lightly sclerotised, and it was not identified with certainty. Fortey & Theron (1995: Table 2, character 6) coded the *Naraoia* hypostome as conterminant (attached) but that of *Misszhouia* is, in their terminology, natant. The hypostome does not have a sutural attachment to cephalic doublure, and no rostral plate is present; hypostomal attachment is by imbedding in soft tissue (see discussion of Ventral Cuticle below).

The presumed homology of the frontal organs in *Misszhouia* is with parts of the median eye complex in other arthropods. The lateral pair of frontal organs may represent the paired ventral frontal organs of Crustacea (Elofsson, 1965). Paulus (1979) speculated that the ventral eyes of xiphosurids may be the homologue of crustacean ventral frontal organs. As such, he hypothesised that a pair of ventral frontal organs—if present in chelicerates as well as crustaceans—were a general condition of the median eye complex in arthropods. Little evidence for frontal organs has been identified in Cambrian arachnates, although a correspondence with the paired reflective spots on the anterior "rostral" sclerite in *Helmetia* should be considered (see Briggs in Conway Morris *et al.*, 1982: pl. E). If so, the anterior sternite of helmetiids might be homologised with the boomerang-shaped, preantennular sternite in *Misszhouia*. A stringent test of homology with ventral frontal organs in extant arthropods is not possible without knowledge of their gangliar innervation (i.e., evidence for protocerebral innervation).

Comparison of the naraoiid frontal organs with the paired, pimple-like swellings in *Agnostus* described as frontal organs by Müller & Walossek (1987) is obvious. These organs similarly lie anterior to what has been described as the hypostome, leading us to speculate that the agnostid "hypostome" might correspond to the ovate lobe of *Misszhouia*, or only *part* of the trilobite hypostome. The view that the maculae of trilobites are ventral eyes (Lindström, 1901) has led to their proposed homology with the ventral eyes of xiphosurids (Størmer, 1934; Müller & Walossek, 1987: 46). It certainly appears unlikely that maculae would be homologous with the frontal organs of *Misszhouia*, given the more posterior position of the former on the main swelling (middle body) of the hypostome (Fig. 7).

Mouth. The anterior part of the digestive tract, the foregut, is rarely preserved in *Misszhouia longicaudata*, but details are well-displayed by specimen ELRC 11559 (Figs 2a, 3b). The mouth is situated at the rear edge of the ovate lobe of the hypostomal complex, and is directed posteriorly. The esophagus is narrow (Fig. 4a), extending only to the anterior edge of the ovate lobe. At this point the digestive tract expands to a much greater width (about three times that of the esophagus) and flexes upward and backward, forming a stomach overlying the esophagus. A pair of small, mud-filled, ovoid swellings are situated just outside the esophagus at a point about two-thirds of its length (from the rear). A mud-filled tube runs from each swelling posteriorly, converging towards and terminating at the mouth opening. We interpret the paired swellings as digestive glands, and the tubes as ducts leading to the mouth. Their homologue in extant arthropods in uncertain.

The configuration of the mouth and foregut in *Misszhouia* is that inferred for trilobite-allied arachnates in general (e.g., Cisne, 1975: fig. 8), but rarely directly observed in fossils. The second cephalic appendage pair is postoral in *Misszhouia* (versus paroral in *Agnostus* and stem lineage crustaceans; Müller & Walossek, 1987: 47); the antennules are the sole preoral appendage pair.

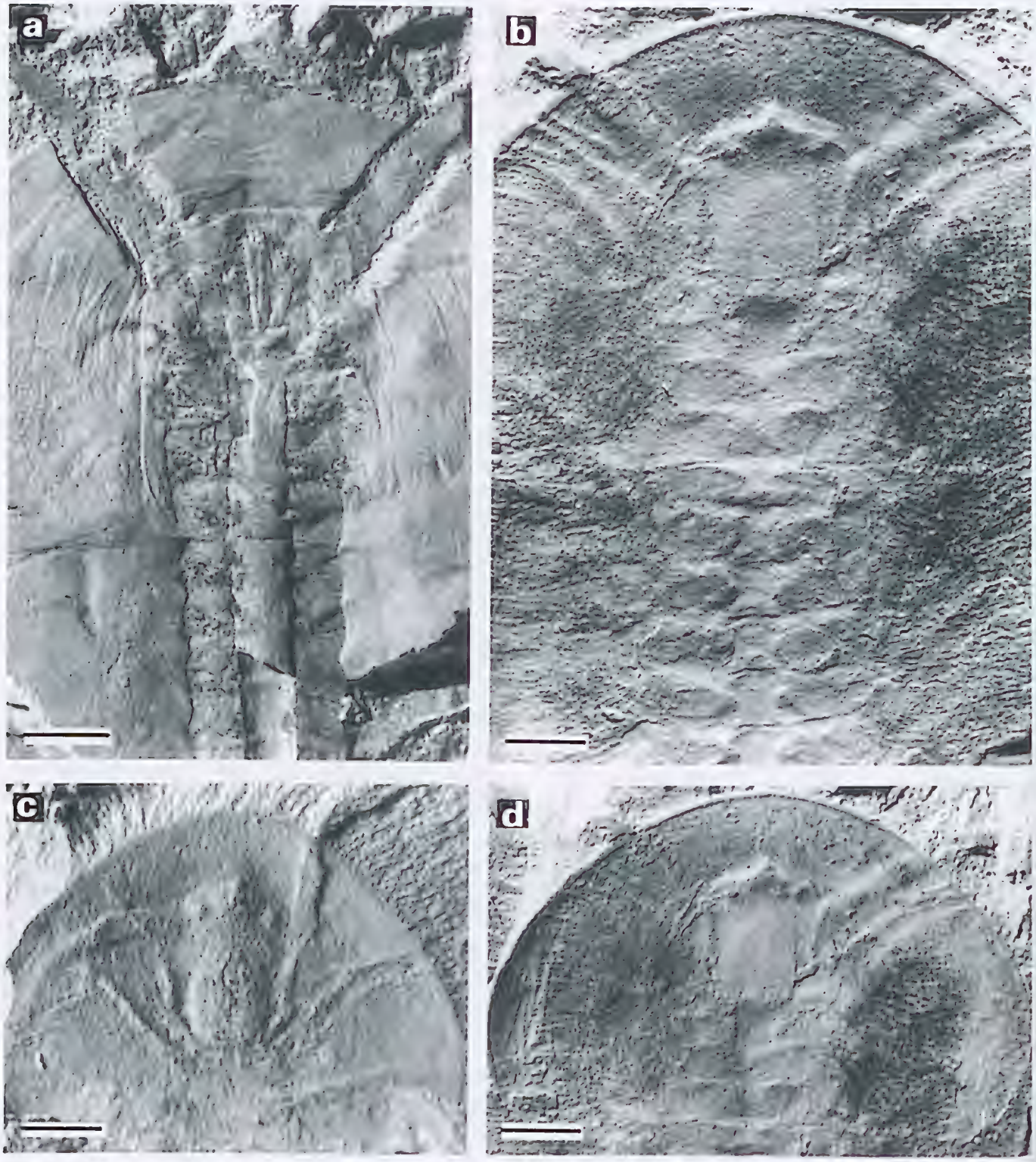

Fig. 2. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11559, from locality MQA, detail of head shield and anterior part of trunk (see Fig. 3b for camera lucida drawing, Fig. 13c for complete specimen). Light from NW. Scale bar 2 mm; b, d, ELRC 11683a, from locality MN5. Ventral views, light from NNW (b), NW (d). Scale bars 2 mm (b) and 3 mm (d); c, ELRC 11558, from locality MQ1, ventral view of head shield (see Fig. 3a for camera lucida drawing). Light from W. Scale bar 1 mm.

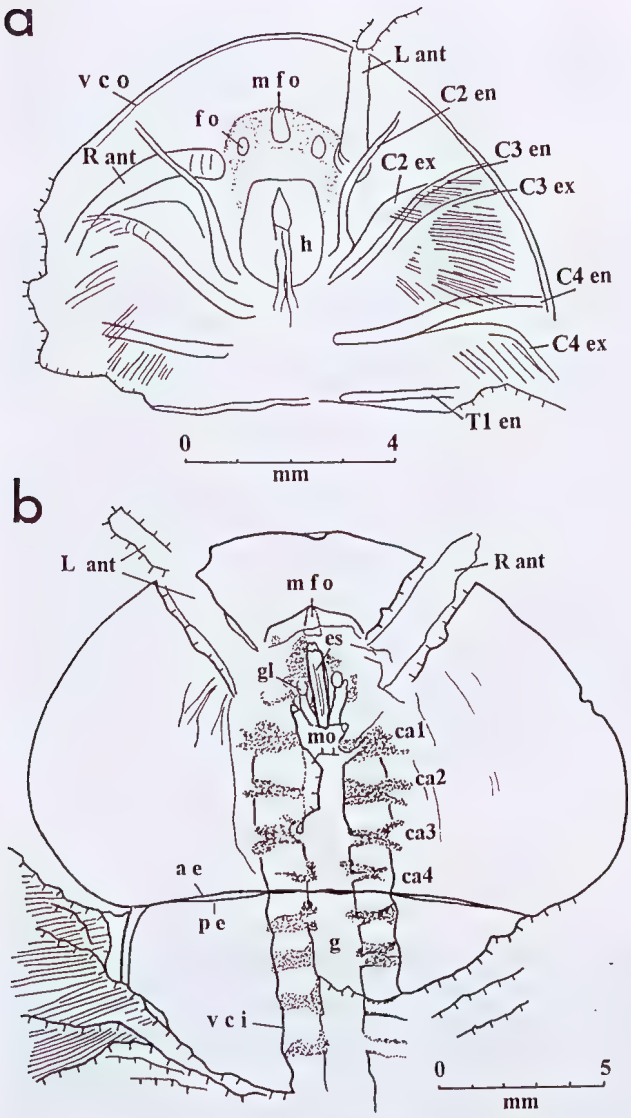

Fig. 3. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, camera lucida drawing of ELRC 11558 (fig. 2c). b, camera lucida drawing of ELRC 11559 (Fig. 2a). See Appendix for abbreviations.

Antennular attachment. As noted above, the antennule is based at the anterolateral edge of the hypostomal complex (Fig. 2). There is considerable separation of the antennules and first post-antennular appendages (Figs 3a, 4). Some specimens show a few folds of arthrodial membrane at the base of the antennule (Figs 4, 8c), and arthrodial membrane or ventral cuticle is continuous from the antennular base to the ovate lobe and the frontal organs.

Whittington (1977) interpreted the antennule of *Naraoia compacta* as attaching anterior to the hypostome, and spaced far in front of the first pair of post-antennular appendages. The separation of the antennule and the first biramous appendage pair is confirmed for *Misszhouia*. There is less disagreement with Whittington's interpretation of the antennules attaching in front of the hypostome than would first appear to be the case because Whittington's "hypostome" (dotted outline in his fig. 96) corresponds to the ovate lobe only. The relative position of the ovate lobe and antennular attachment shown by Whittington for *Naraoia compacta* is closely comparable to that of *Misszhouia*. The shape of antennomeres is also similar in *Naraoia compacta* and *Misszhouia* (Fig. 5b), these being wider than long proximally, and longer than wide distally.

Midgut caeca. Four pairs of lateral diverticula or gut caeca are present in the cephalon of *Misszhouia longicaudata* (Figs 2a, 3b). They are preserved as reddish-brown stains, extending laterally from the gut, and bifurcating distally. In specimens where the gut is mud-filled (Fig. 2a), the mud has also penetrated some distance into the caeca. The dark stain of the caeca is preserved both on the dorsolateral and ventrolateral sides of the gut, showing that the caeca had a complex set of small-scale ramifications of considerable dorsoventral extent. The cephalic caeca are equally-spaced relative to each other and of about equal size. The first caecum branches from the gut at the rear edge of the hypostome, i.e., directly dorsal to the mouth (Fig. 3b). Midgut caeca are comparably developed in the anterior part of the trunk, but become smaller and less defined behind the first five trunk segments.

This concentration of midgut caeca in the cephalon and anterior part of the trunk is a general character for a broader group including trilobites. Distantly related trilobites such as *Pterocephalia* (Chatterton *et al.*, 1994) and *Eoredlichia* (Shu *et al.*, 1995: fig. 15A,B) display a particular concentration of gut caeca in the cephalon and first few thoracic segments. The functional basis is evidently for chemical processing (enzyme production and absorption of nutrients) to occur well in front of the end of the gut.

Biramous limb attachment. The attachment sites of the post-antennular cephalic and trunk appendages are marked by a few strong, concentric, ovoid annulations (Figs 8a, 9a). The attachment site is larger in area than had been inferred to be the case for *Naraoia compacta* (Whittington, 1977) and for trilobites, but is smaller (relative to the size of limb base) than that observed in *Agnostus* (Müller & Walossek, 1987) and stem lineage crustaceans (Walossek & Müller, 1990). The annulations are regarded as a partially sclerotised, arthrodial membrane which connected the proximal podomere of the leg (the basis according to Walossek, 1993, 1995—not the "coxa", as has traditionally been inferred) to the body. This arthrodial membrane permitted considerable movement of the leg and proximal flexibility that has not been recognised in prior reconstructions of *Naraoia* or trilobites.

Walossek (1993, 1995) clarified homologies between the basis and limb rami (endopod and exopod) in Crustacea and early arachnates (Ramsköld & Edgecombe, 1996). The annulated arthrodial membrane to which the basis attaches in *Misszhouia* displays a resemblance to the attachment of the basis to the body in stem lineage crustaceans, such as *Martinssonia* (Walossek &

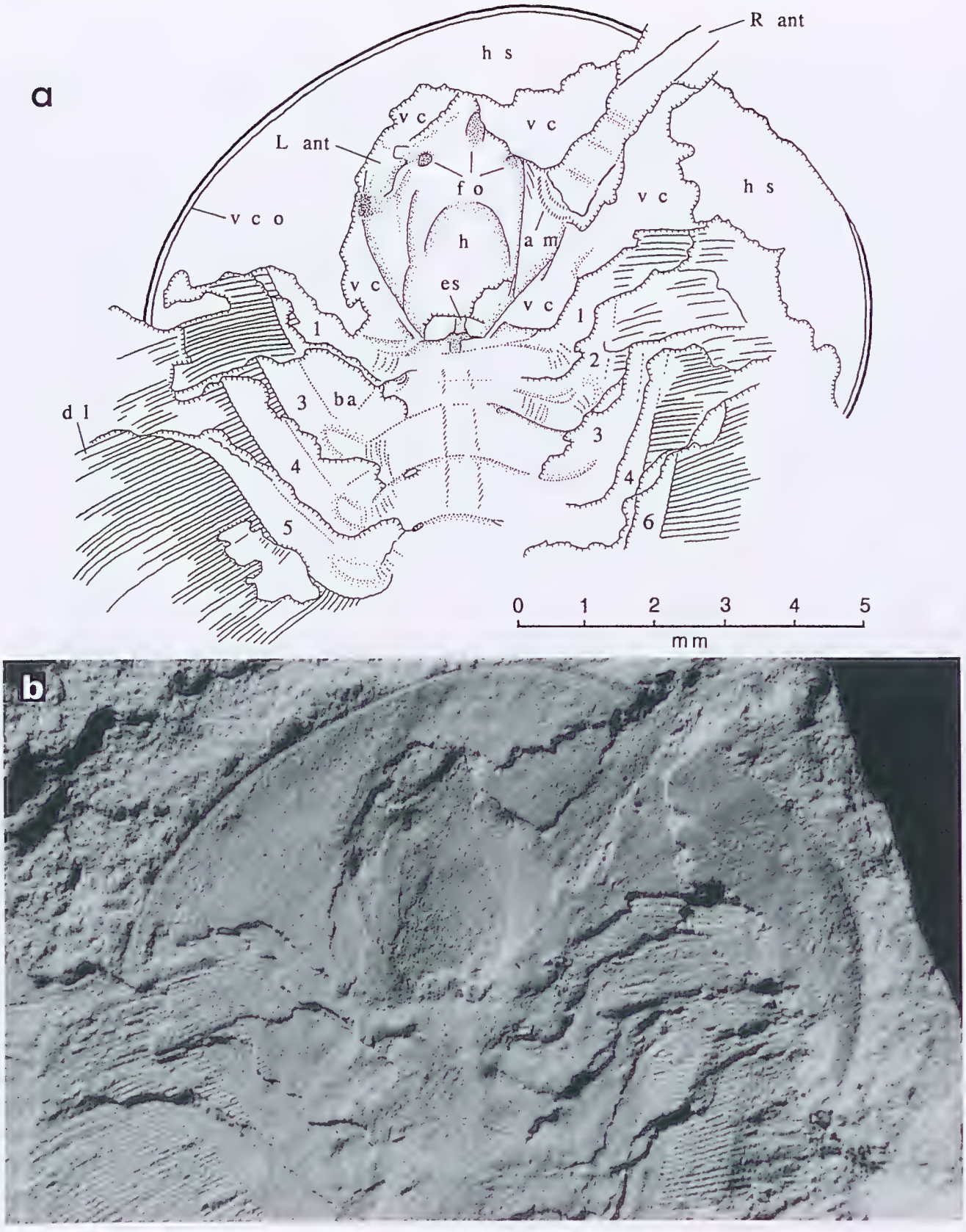

Fig. 4. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, camera lucida drawing of head and anterior part of trunk of ELRC 11076a, from locality MQA. The specimen was embedded in the sediment tilted to the right side, so that ventral structures are displaced to the left. The biramous limbs are numbered 1 to 5 from anterior on the exopod shafts. See Appendix for abbreviations; b, ELRC 11076a. Light from NW (see Fig. 10b for trunk).

Szaniawski, 1991: fig. 7D). This suggests that the proximal articulation of the leg (proximal part of the basis) is homologous across the Crustacea and Arachnata. Disarticulated limbs of *Misszhouia longicaudata* (Figs 5d, 6, 11, 12) show that the proximal articulation is a sharply defined feature.

Tergite overlap. The overlap of the anterior edge of the trunk by the head shield is slight (Figs 2a, 3b), being clearly expressed on the pleural region, and no exoskeletal articulating structures are developed. Whittington (1977: fig. 96) reconstructed a much longer area of overlap between the tergites in *Naraoia compacta*.

Sternites. Between the attachment sites of all biramous appendages are hourglass-shaped sternites (Figs 8a, 10a, 13a). Three cephalic sternites are present behind the hypostome, these being progressively shorter (sag.) anteriorly and shorter than those along the trunk (Fig. 9a). There is little evidence for structural differentiation of the associated cephalic limbs, other than the generally more slender endopod and exopod shaft, notably on the first post-antennular limb (Figs 2c, 9c). The exopod fan on the first two pairs of biramous limbs is developed in a similar manner to that on the third, rearmost cephalic limb and the trunk limbs.

The presence of sternites associated with each of the post-antennular limbs in *Misszhouia* is similar to the presumed primitive chelicerate condition. In palpigrades, for example, sternites are associated with the chelicerae (I), pedipalps and third legs (II + III plate), and each of the remaining prosomal limbs (IV–VI) (Snodgrass, 1952: fig. 23B). Consequently we identify a complete set of post-antennular sternites as a general state for Arachnata. This provides another difference from *Agnostus*, which lacks an antennal (second cephalic) sternite (Müller & Walossek, 1987).

The region between the leg attachment sites in the trilobite *Placoparia* (Whittington, 1993: fig. 4) is very similar to that of *Misszhouia*, suggesting that trilobites could have had sclerotised but unmineralised sternites between the leg attachments. Trunk sternites of anomalocaridids (Hou *et al.*, 1995: figs 9, 10) are generally similar in outline to those of *Misszhouia*. Accordingly, we regard this sternal form as widespread throughout the Arthropoda.

Intersegmental tendons. Between the sternites and appendage attachment sites run narrow bands interpreted as transverse tendinous bars. These components of the general euarthropod intersegmental tendon system (Boudreaux, 1979) have also been identified in trilobites (Whittington, 1993). The tendinous bar between the third and fourth postoral sternite, i.e., at the position of the head/trunk juncture, is marked by a transverse fold (Ramsköld *et al.*, 1996: fig. 2B), indicating the point of flexure (Fig. 9a). Each of these sternites is associated with an appendage pair, and from this point of view, the cephalon has three postoral appendage pairs. In dorso-ventral view, the fourth sternite extends across the articulation between the head and the trunk, about equally far in both directions or perhaps a bit further anteriorly. Functionally, however, the sternite would have been part of the trunk rather than the head. The boundary between the head and trunk, when traced through a cross-section of the animal, would thus not be vertical but an anteroventrally inclined plane.

Exopod. The exopod shaft of *Misszhouia longicaudata* is relatively narrow along its entire length. It is, however, notably widest proximally, and gently tapers distally (Figs 11, 12, 13a). Imbricating, flattened setae articulate to the rear edge of the exopod shaft along most of its length (i.e., in that extent homologous with the inner lobe of the exopod in trilobites such as *Olenoides* and *Eoredlichia*). The lamellar setae are usually more or less straight or slightly curved, indicating that they were fairly stiff, although some specimens demonstrate post-mortem deformation of the setae (Figs 5d, 6, 12b). A distal lobe is set off from the main shaft of the exopod by a transverse articulation (Fig. 13d). The lobe is lanceolate rather than markedly expanded as in *N. compacta*. The distal lobe typically bends backwards to parallel the course of the lamellar setae on the main shaft of the exopod (Figs 4a, 8b, 11), and bears many short, densely packed bristles along its outer edge (Fig. 8d).

The imbrication of the setae is clearly seen in several articulated specimens. In dorsal view, the scarp of each seta is directed outward, showing that the setae underlie each other outward (see lower right side in Fig. 11a). The proximal edge of the distal lobe is thus overlapped by a few setae in dorsal view, but is fully exposed in ventral view. This imbrication and difference in exposure of the distal lobe enables an unambiguous orientation also of isolated limbs. The specimen figured by Chen *et al.* (1991: fig. 6) shows the distal lobe partly overlapped by setae, and is thus seen in dorsal view (Fig. 12a). An isolated limb figured herein (Figs 11, 12b) shows the distal lobe fully exposed, and is a ventral view. The orientations are confirmed by the imbrication seen elsewhere in the exopod fan. An important difference between limbs seen in dorsal and ventral view is the shape of the proximal margin of the basis and the exopod shaft. In dorsal views this line forms a gentle embayment, whereas in ventral views the embayment is much deeper. This difference reflects the attachment of the articulating membrane and other tissues.

The exopod was attached along the entire length of the basis (Fig. 12), and this attachment extends onto at least the proximal part of the first podomere of the endopod. A strong attachment of the immense exopod "fan" by extending the length of its hinge along the basis is an obvious characteristic of *Misszhouia*. Ramsköld & Edgecombe (1996) proposed that such a hinge—the exopod connected with the entire length of the basis—is a more general character, shared with primitive Trilobita.

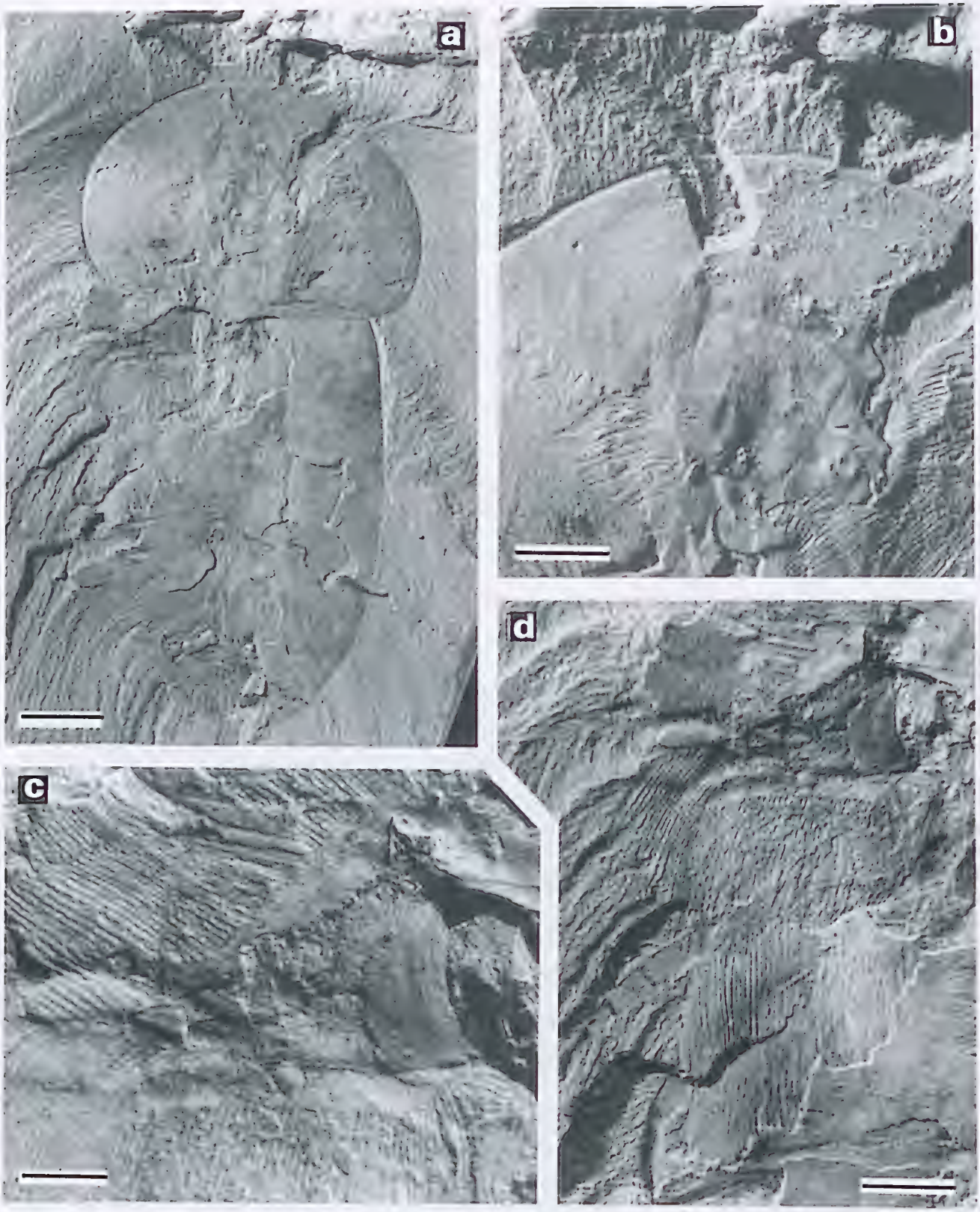

Fig. 5. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11940, from locality MN4, all dorsal views. a, complete specimen, showing several disjointed, displaced, and overturned limbs. Light from WNW. Scale bar 4 mm; b, detail of cephalon, showing left antennule prepared beneath head shield. Light from NW. Scale bar 2 mm; c, appendages in anterior part of trunk on left side of specimen, showing basis and endopod in an approximately non-displaced position (appendage "X" in Fig. 6). Note sharply defined proximal edge of basis. Light from NNE. Scale bar 1 mm; d, anterior appendages on left side of trunk (see Fig. 6 for camera lucida drawing). Light from NNW. Scale bar 2 mm.

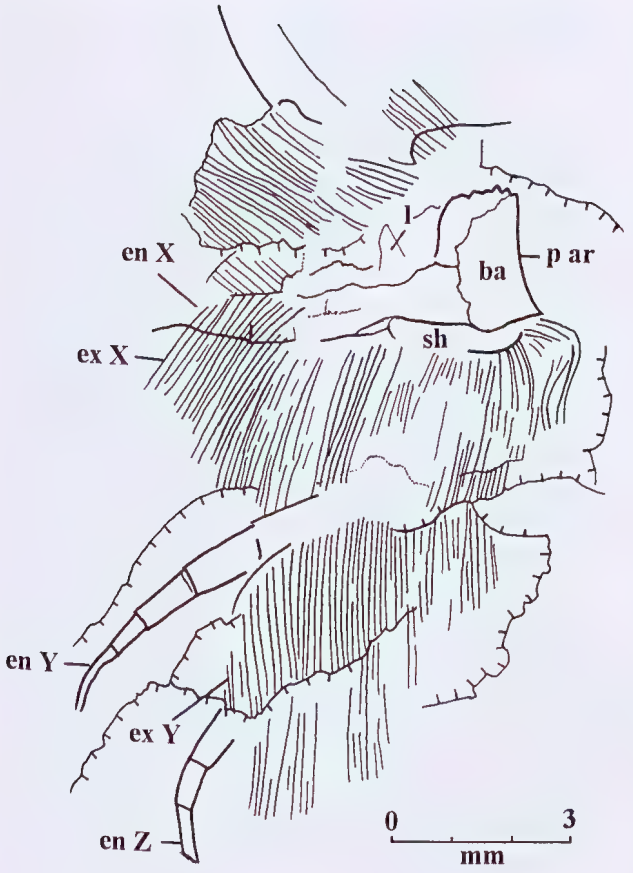

Fig. 6. *Misszhouia longicaudata* (Zhang & Hou, 1985). Camera lucida drawing of trunk appendages in specimen ELRC 11940 (Fig. 5d). See Appendix for abbreviations. "1" refers to endite on first podomere of endopod. Line separating basis and first podomere of endopod is a fracture rather than a joint. Three appendages labelled "X", "Y" and "Z".

Endopod. The basis and the first podomere of the endopod appear to have a non-functional joint, because a well-developed articulation has not been detected (Figs 11, 13b, 14). The first podomere is shortened, being about 60 percent the length of the second podomere, and is unique in its development of a strong, angular endite. Podomeres 2–4 are each of about equal length, whereas podomeres 5 and 6 are 70 percent the length of these. The terminal (seventh) podomere is a stout claw.

The discovery of seven podomeres in the endopod of this naraoiid (Fig. 12), versus six in *Naraoia compacta* (Whittington, 1977) allows the possibility of precise homologies between all podomeres in the endopod of *Misszhouia* and that of trilobites (Müller & Walossek, 1987: fig. 27).

Ventral cuticle. The term ventral cuticle is here used for the lightly sclerotised integument protecting the internal tissues on the ventral side of the animal. This delicate structure is virtually never preserved in fossilised arthropods, the only major exception being phosphatised material such as the Upper Cambrian Orsten fauna (e.g., "inner lamella" of Müller & Walossek, 1987). Some specimens of *M. longicaudata* may be the first to show significant portions of it in non-phosphatised fossil arthropods, due to the split of the rock which has passed, is smaller or larger areas, along the ventral cuticle.

In the distal areas, the surface of the ventral cuticle is smooth and featureless (Fig. 4). Some small folds (which are presumably preservational) are seen both perpendicular to the margin in the trunk (Fig. 9b), and parallel to the margin of the head shield (Fig. 9c; see section on Doublure). Embedded in the ventral cuticle, without clearly defined margins, are structures such as the components of the hypostomal complex. Where

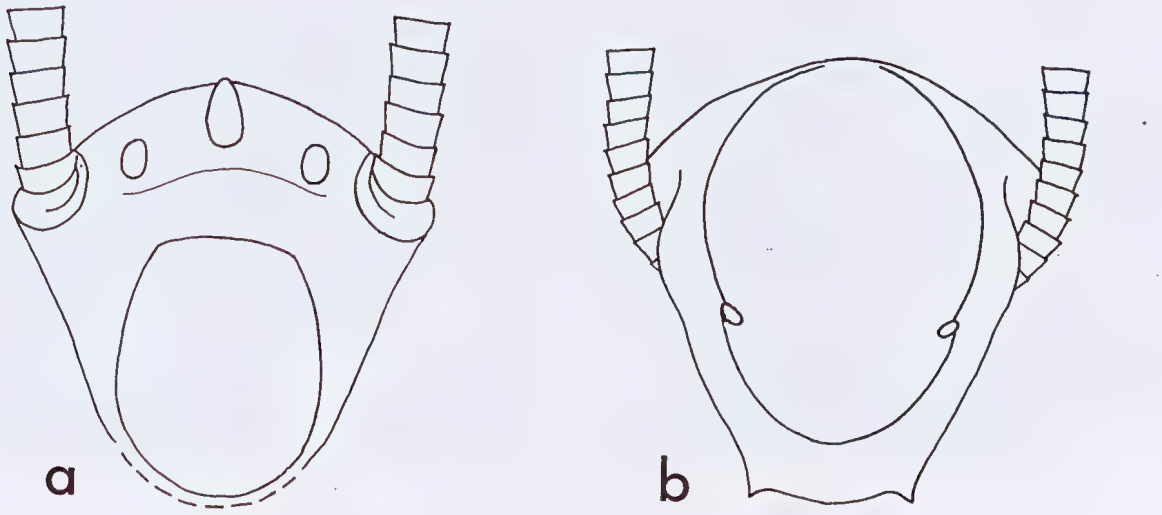

Fig. 7. Comparison of naraoiid and trilobite hypostomes, showing antennular attachments. a, *Misszhouia longicaudata*; b, *Ceraurinella*. Morphology and orientation of antennules based on *Triarthrus* (Whittington and Almond, 1987).

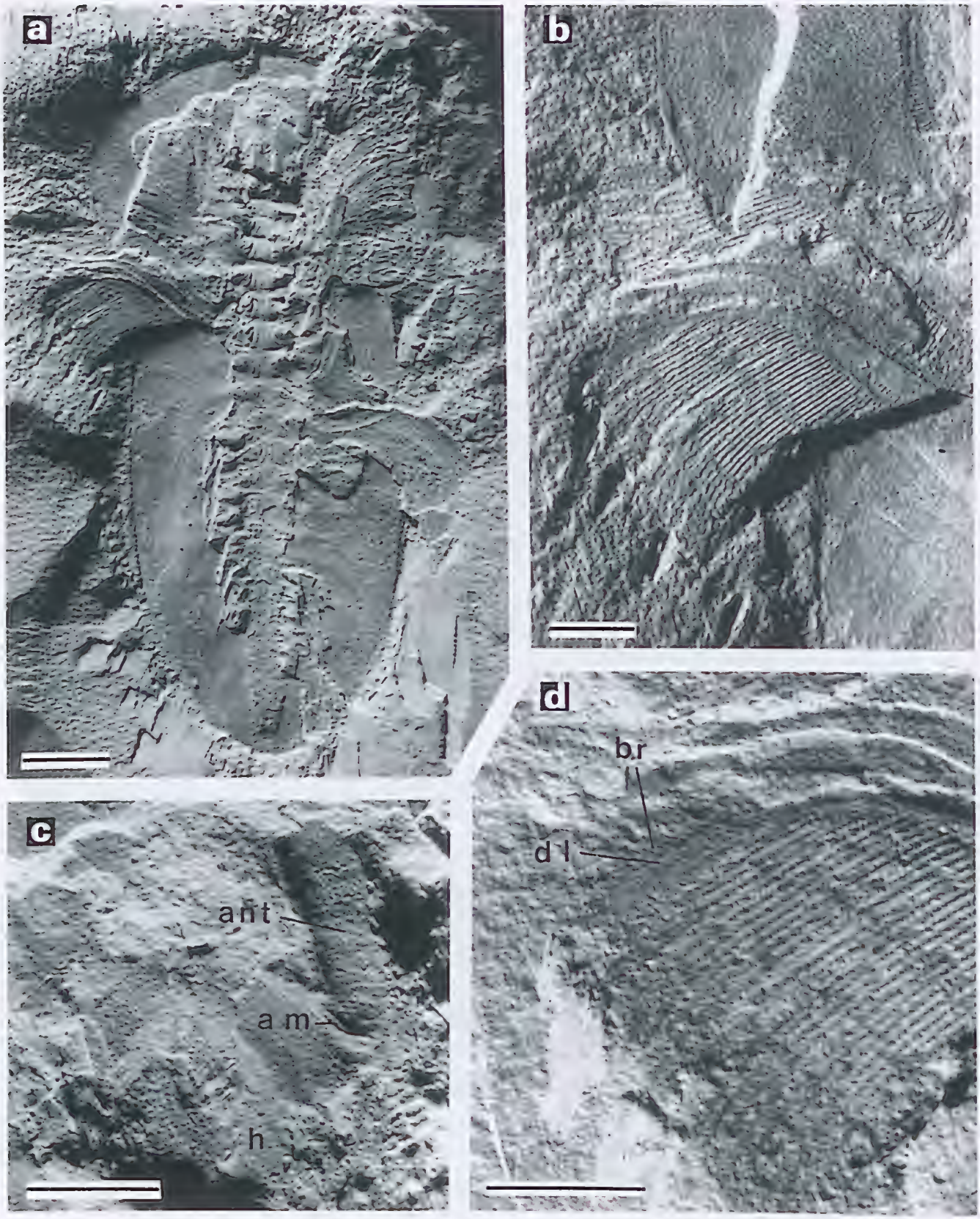

Fig. 8. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11590b, all ventral views (see Ramsköld *et al.*, 1996: fig. 2 for counterpart). a, complete specimen. Light from NNW. Scale bar 5 mm; b, detail of left side, showing appendages in anterior part of trunk. Light from WNW. Scale bar 2 mm; c, detail of hypostomal complex, showing attachment of antennule (ant), arthrodial membrane (a m) and ovate lobe of hypostomal complex (h). Light from N. Scale bar 2 mm; d, detail of distal part of appendage in Fig. b. Bristles (br) on outer edge of distal lobe of exopod (d l) are indicated. Light from NNE. Scale bar 2 mm.

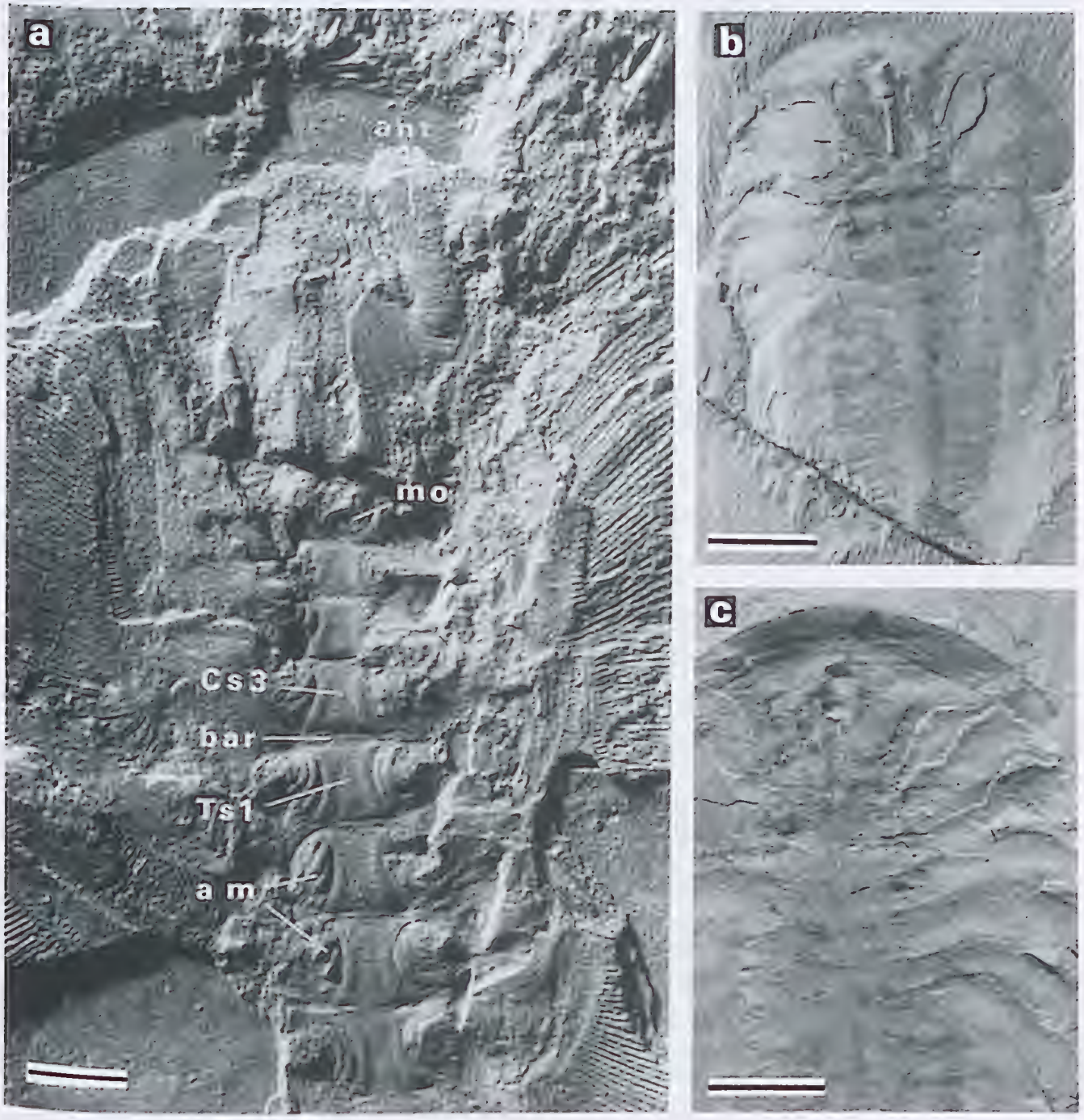

Fig. 9. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11590b, detail of cephalon and anterior part of trunk (see Fig. 8 for additional views) in ventral view. See appendix for abbreviations. "bar" is tendinous bar at juncture between third cephalic sternite (Cs3) and first trunk sternite (Ts1). Position of mouth (mo) approximate. Light from NW. Scale bar 2 mm; b, c, ELRC 11684, from locality MQ1. b, ELRC 11684a, dorsal view, specimen exposing ventral cuticle in much of the cephalon and on right side of trunk. Mud-filled esophagus appears to extend too far posteriorly to accurately show position of mouth at its posterior end, and part of the digestive tract shown in relief may belong to the midgut. Light from NNW. Scale bar 4 mm; c, ELRC 11684b, ventral view, detail showing ventral cuticle in the cephalon. Note the position of the relatively small exopods of the first post-antennular cephalic appendage pair (left one complete). Light from NW. Scale bar 3 mm.

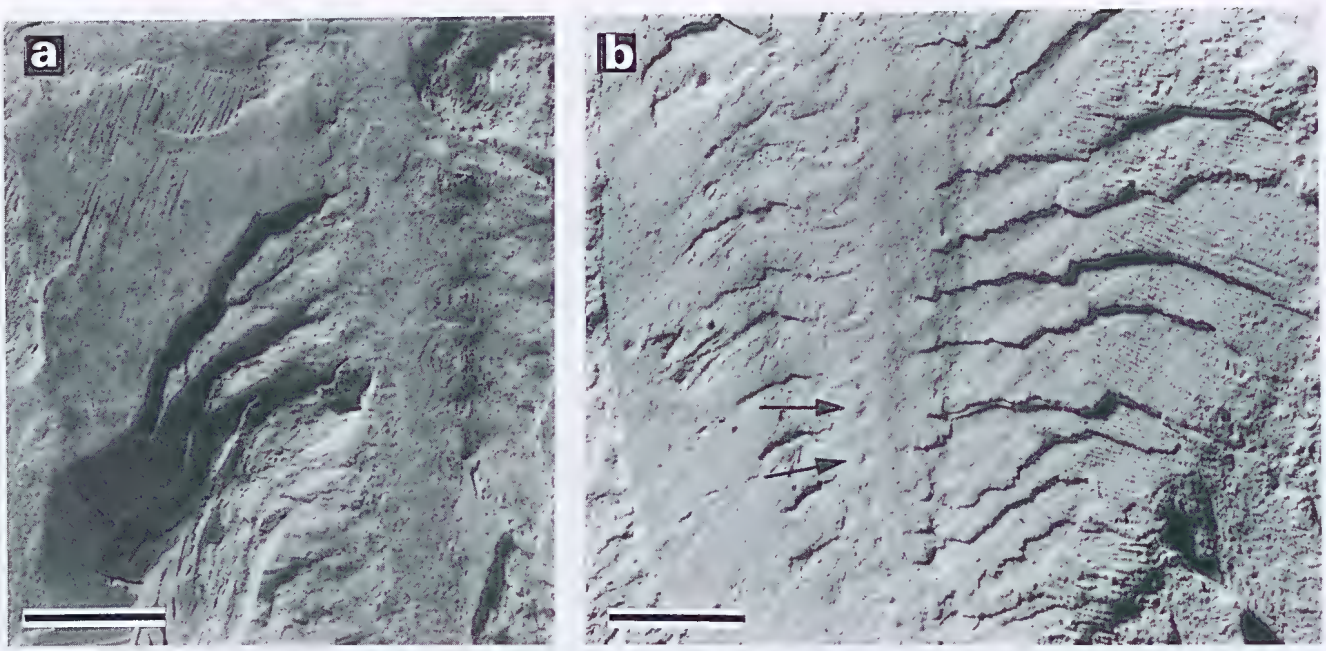

Fig. 10. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11590a, posterior part of trunk in dorsal view (detail of Ramsköld *et al.*, 1996: fig. 2a, after preparation of trunk limbs. See Fig. 8a for counterpart). The split has passed along the ventral surface of the trunk stem. Light from NNW. Scale bar 3 mm; b, ELRC 11076a, from locality MQA, trunk in dorsal view (see Fig. 4 for head and anteriormost part of trunk). The split has passed through the body at a plane immediately below the dorsal exoskeleton. Arrows point to paired axial impressions where dorsoventral musculature attached to the ventral side of the exoskeleton. Light from NW. Scale bar 2 mm.

movable structures, such as the antennules, are based in the ventral cuticle, the cuticle forms a series of concentric annuli around their base (Figs 3a, 4, 8c). These annuli show that the cuticle was not sufficiently elastic in itself to permit major deformation, but that flexibility had to be achieved by folding rather than through stretching and contraction.

In the lateral two-thirds, the ventral cuticle roughly followed the convexity on the dorsal shields (Figs 9b, 10b). Adaxially, in the limb-bearing part of the animal the cuticle flexed abruptly ventrally to surround the limb bases that extend laterally from the axial trunk stem. The adaxial limit of the ventral cuticle, that is, the adaxialmost extent of mud penetration between the cuticle and the exopods, is commonly sharply outlined in the specimens, seen as a gently undulating, exsagittal line (Figs 2a, 3b). The cuticular covering on the ventral side of the axial trunk stem consists of sternites with annulated ventral cuticle between the the limb bases and the sternites.

Doublure. The ventral cuticle attaches laterally on the ventral side just inside the margin of the head and trunk shields. Mud has penetrated inside the tissues up to the line of attachment, which can be seen in many specimens as a line parallel to the margin of the tergites (Figs 2b,d, 4), effectively leaving only the thickness of the dorsal shield outside the line. In *Naraoia compacta*, this line has previously been interpreted as the margin of a very narrow doublure (Whittington, 1977: 421–422). There is no evidence in either *Naraoia* or *Misszhouia* of a doublure in the sense of the margin of the tergite being flexed or rolled under to form a continuation of the sclerotised shield on the ventral side.

Other lines seen parallel to the margin of the shields in the fossils can also be rejected as candidates for a doublure margin. In the head shield, a line about 15 percent of the shield diameter is sometimes seen in both *N. compacta* (Whittington 1977: pl. 3, figs 16–20) and *M. longicaudata* (Fig. 9b,c). In *N. compacta* the line coincides with the distal extent of the diverticula, but since *M. longicaudata* lacks such diverticula, the line may represent the inner limit of a somewhat strengthed portion of the ventral cuticle. This is not, however, closely comparable to a doublure as defined above. Another line, or scarp, is seen even further adaxially in some specimens of *N. compacta* (Whittington 1977: pl. 2, figs 9–12). This line is clearly situated on the dorsal shield rather than on the ventral side and is a postdepositional artifact caused by compaction which exaggerated the limits of the axial region.

Relationships

With the above morphological considerations, several characters are identified that separate *Misszhouia longicaudata* as sister to a clade including *Naraoia compacta* and *N. spinosa*. We

infer that *N. spinifer* Walcott, 1931, belongs to this latter clade, based on the pervasive similarity of its exoskeletal features to those of *N. spinosa*. Given the inadequate state of knowledge of its soft anatomy, however, the systematic position of *N. spinifer* is not further explored here.

Implicit in this consideration of relationships is the monophyly of Naraoiidae sensu Fortey & Theron (1994). We endorse several characters identified as naraoiid synapomorphies by Fortey & Theron (1994: 842)—the transversely oval or semicircular head shield, lack of dorsal eyes, and the pygidial tergite exceeding the length of the head shield. To this list of synapomorphies uniting *Liwia, Naraoia, Misszhouia, Tariccoia*, and *Soomaspis*, we add a unique aspect of tagmosis, the distinctive narrowing of the anterior part of the trunk relative to the head shield and posterior part of the trunk. This condition is observed in naraoiids regardless of the presence or absence of trunk articulations. The hypothesis that Naraoiidae is a monophyletic group (Fig. 15) means that notions of a paraphyletic "nectaspid" grade as ancestral "soft-bodied trilobites" (Shu *et al.*, 1995: fig. 20B) should now be abandoned. Phylogenetic analyses will be better served by considering the internal components of "Nectaspida" (e.g., Naraoiidae, Tegopeltidae) as separate terminal taxa.

Within this context of a naraoiid clade, synapomorphies of *Naraoia* (*compacta* + *spinosa*) that exclude *Misszhouia longicaudata* are:

1. large, ramifying anterior pair of digestive diverticula in the cephalon. These are well known for *N. compacta* as well as *N. spinosa* (Figs 16a,c, 17, 18b, 19), in which they are typically mud-filled in relief, and occupy most of the genal region. In *Misszhouia longicaudata*, four pairs of relatively small caeca are present in the cephalon (Figs 2a, 3b) all of which bifurcate distally. The anterior pair of caeca are not differentiated in size, a situation in striking contrast to *Naraoia*;

2. bloated, mud-filled gut. The width of the gut of *Naraoia compacta* (Whittington, 1977: figs 54, 64) and *N. spinosa* (Figs 18b, 19) exceeds that of *Misszhouia longicaudata* (Fig. 18a) by a considerable degree, indeed to an extent not matched by other Chengjiang arthropods (see discussion in "Ecological disparity" below). The bloated, mud-filled gut of *Naraoia* is thus regarded as a shared derived state;

3. laterally deflected antennules. The antennule of *Misszhouia* runs anterolaterally from the hypostome (Figs 2–4, 8c), lacking the strong lateral deflection present proximally in *N. compacta* (Whittington, 1977, figs 5, 49, 51, 60) and *N. spinosa* (Figs 16a,b, 17, 22a, 23). The antennules in *Misszhouia* were evidently capable of rotation at their attachment, allowing a somewhat lateral orientation (compare Figs 2b and 8c for range of variation), whereas in *N. spinosa* the antennules were forced to flex anteriorly far distal to their attachment in order to reach an exsagittal direction (Fig. 16b), but the proximal part consistently runs transversely from the hypostome. Relevant outgroup taxa such as Trilobita (Whittington & Almond, 1987; Shu *et al.*, 1995), Tegopeltidae (Whittington, 1985: figs 2, 3), and Helmetiida (Hou, 1987: pl. 3, fig. 2) also lack a strong proximal deflection of the antennule. The apomorphic state in *Naraoia* is also shared by *Liwia* which, contrary to its reconstruction (Dzik & Lendzion, 1988: fig. 5A), has strongly deflected antennules (Dzik & Lendzion, 1988: fig. 4A,B).

Based on these synapomorphies, characters shared by *Misszhouia longicaudata* and *Naraoia compacta* (e.g., a massive ventral projection on the first podomere of the endopod, a state unknown for *N. spinosa*) are interpreted as plesiomorphies for a broader clade uniting the two genera. This prediction is supported by the presence of such an endite in outgroup taxa, such as the primitive trilobite *Eoredlichia* (Ramsköld & Edgecombe, 1996).

The exopod of *Naraoia spinosa* is observed to have a paddle-like distal lobe in at least some appendages, e.g., those in the anterior part of the trunk (Figs 16d,e, 17). An expanded distal lobe in *N. compacta* and *N. spinosa* is regarded as a symplesiomorphy, given that basal trilobites (*Eoredlichia* and *Olenoides*) likewise possess a distal lobe (Ramsköld & Edgecombe, 1996) fringed with bristles. As such, the lanceolate distal lobe of *Misszhouia* is regarded as the derived condition, modified from the large, flattened lobe possessed by the common ancestor of trilobites and naraoiids.

The prior classification implies that *Misszhouia* and *Naraoia* are closest relatives within the Naraoiidae sensu Fortey & Theron (1994). The lack of free thoracic segments provides the most obvious synapomorphy to distinguish this clade from *Liwia, Tariccoia*, and *Soomaspis* (character 4 in Fig. 15a). The monophyly of a grouping of these latter three genera ("Liwiinae" sensu Fortey & Theron, 1994) is, however, dubious, being based exclusively on the primitive retention of trunk articulations. Notably, *Liwia* shares lateral deflection of the antennules with *Naraoia*. This putative synapomorphy (character 5 in Fig. 15b) is in conflict with the grouping of *Naraoia* and *Misszhouia* on the basis of trunk fusion. Additional characters from poorly-known taxa (such as *Liwia*) will be required to resolve the incongruence. In contrast to the alternative phylogenies suggested by Fortey & Theron (1994: text-fig. 2), which relied on a single character (number of trunk articulations), we suggest that the Ordovician naraoiids *Tariccoia* and *Soomaspis* are each others' closest relative. Synapomorphic for this group are an extreme widening of the doublure (Hammann *et al.*, 1990: text-fig. 4b; Fortey & Theron, 1994: text-fig. 1A) that is not observed in the other naraoiids (cf. *Misszhouia longicaudata*; Fig. 2b;d), and the development of a median keel on the pygidium.

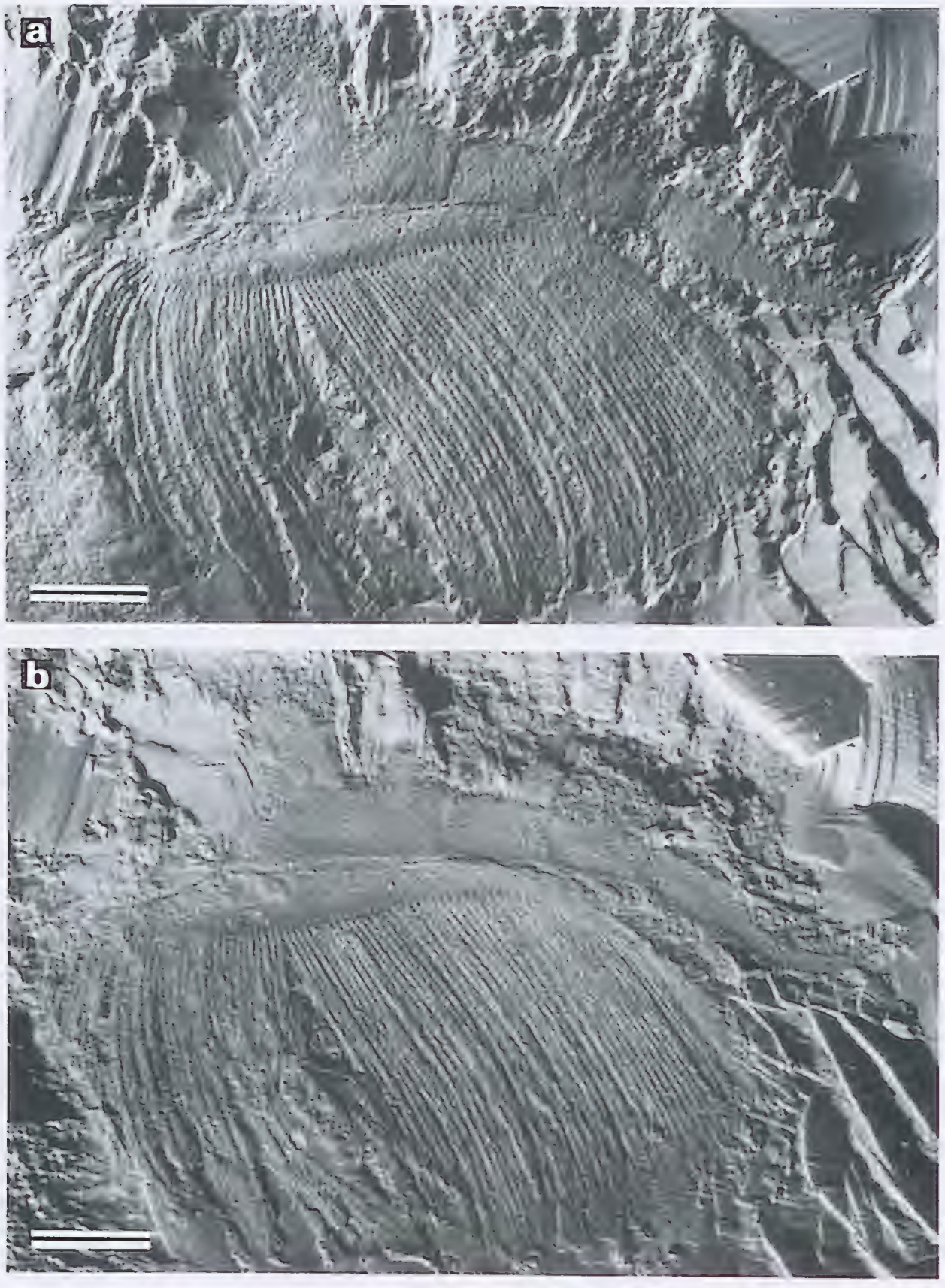

Fig. 11. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 1300a, from locality MW2, ventral view (see Fig. 12b for camera lucida drawing). Scale bars 2 mm. a, very low light from WNW, emphasising podomere joints in endopod; b, low light from ENE, emphasising proximal edge of basis and exopod shaft, joint between exopod shaft and distal lobe, and tip of endopod.

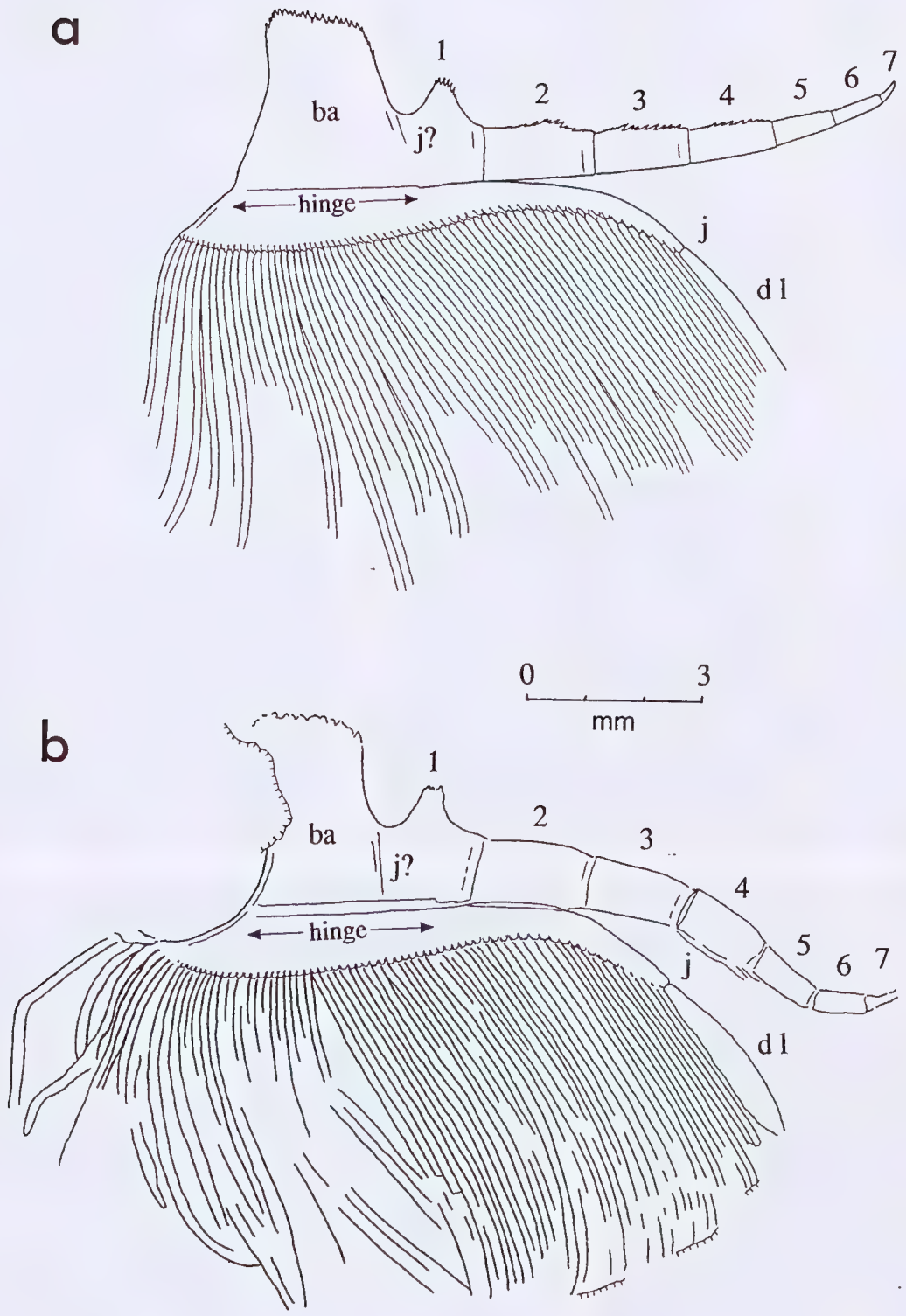

Fig. 12. *Misszhouia longicaudata* (Zhang & Hou, 1985). Interpretive line drawings of limbs preserved disarticulated from the body. Endopod podomeres are numbered 1 to 7. a, specimen figured by Chen *et al.* (1991: fig. 6), dorsal view; b, ELRC 1300a (Fig. 11), ventral view. See Appendix for abbreviations. "j" indicates joint between exopod shaft and distal lobe, "j?" is linear depressions possibly indicating a fused joint between the basis and the first podomere of the endopod.

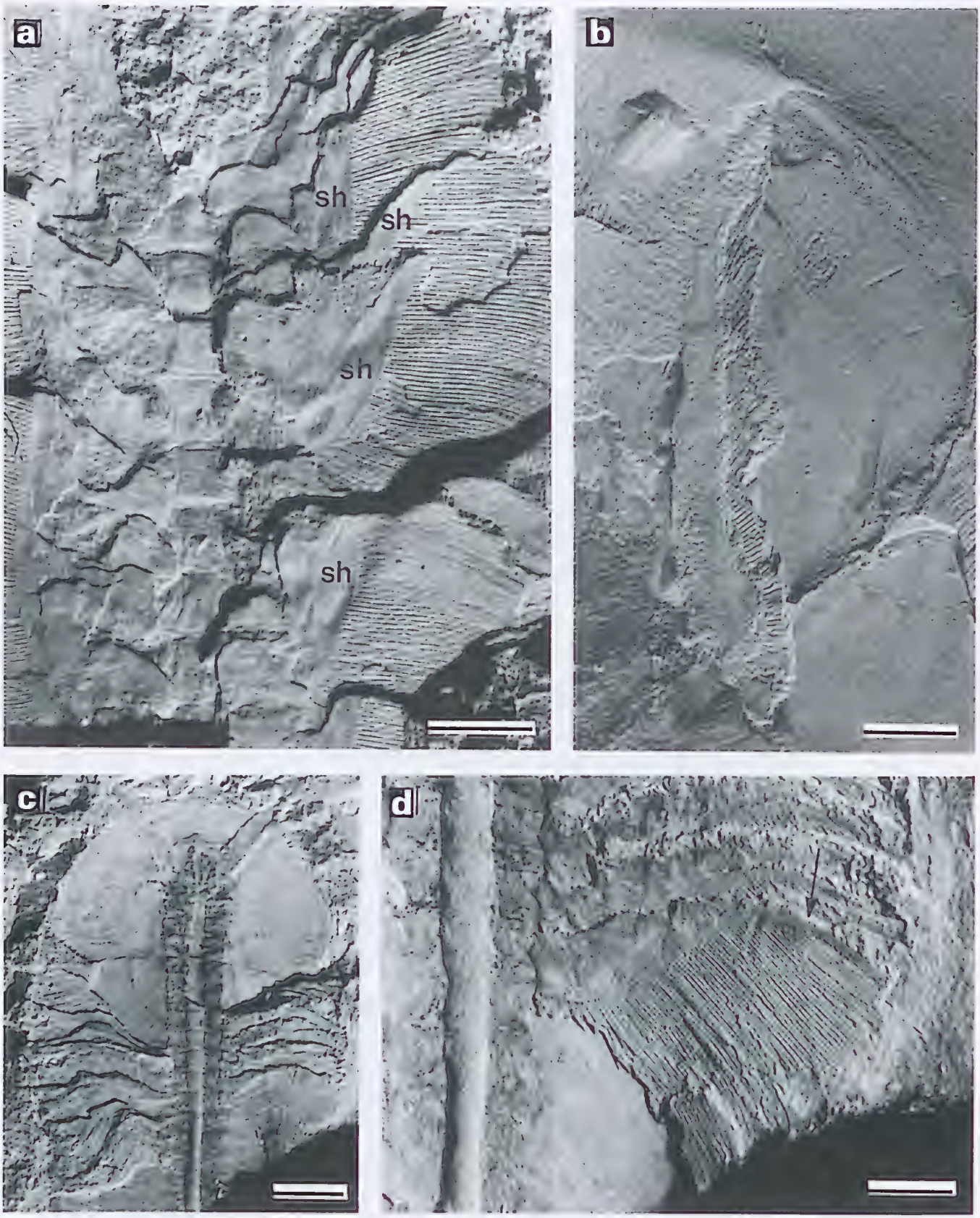

Fig. 13. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11555, from locality MW2, dorsal view of specimen with exoskeleton removed. "sh" indicates exopod shafts. Light from N. Scale bar 2mm; b, ELRC 11561a (see Fig. 14 for camera lucida drawing; see Ramsköld *et al.*, 1996: fig. 1A for counterpart), dorsal view. Exposed endopod is that of first trunk limb. Light from NW. Scale bar 2 mm; c, d, ELRC 11559, from locality MQA. c, view of entire specimen. Light from NW. Scale bar 5 mm; d, detail of trunk, showing mud-fill removed from gut. Arrow indicates articulation of distal lobe of exopod. Light from W. Scale bar 2 mm.

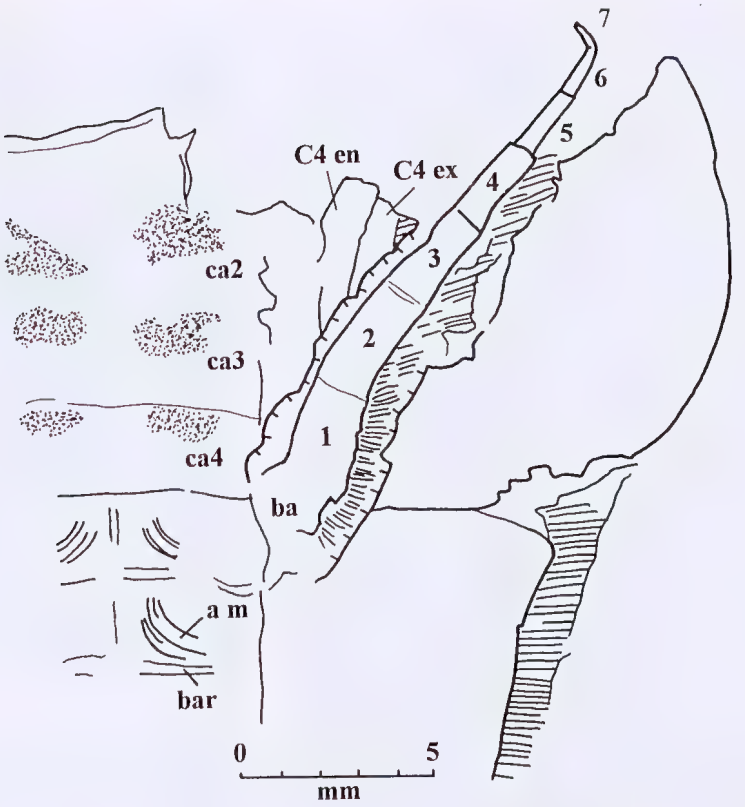

Fig. 14. *Misszhouia longicaudata* (Zhang & Hou, 1985). Camera lucida drawing of ELRC 11561a (see Fig. 13b). Labelled endopod is that of first trunk limb; the exopod "fan" along its posterior edge belongs to the last cephalic limb ("C4 ex"). See Appendix for abbreviations. Endopod podomeres are numbered 1–7.

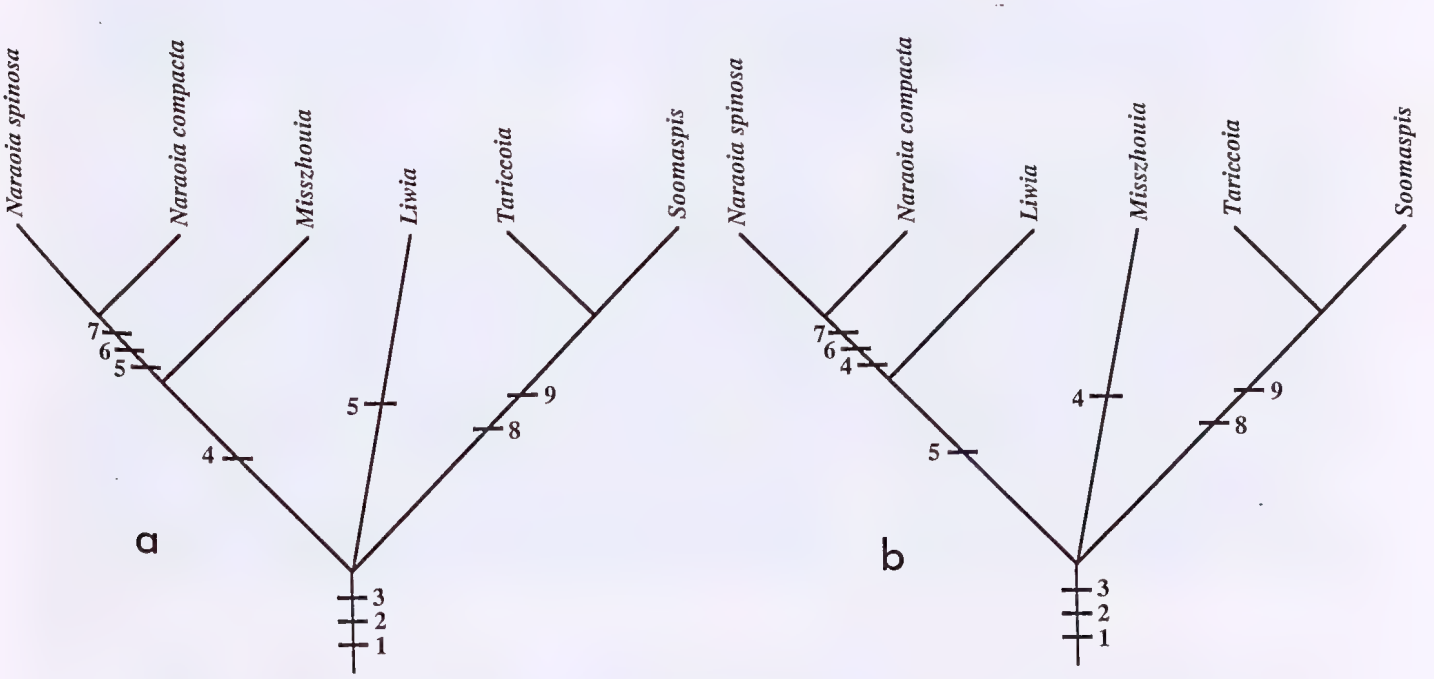

Fig. 15. Alternative cladograms of relationships within Naraoiidae, showing either *Misszhouia* (a) or *Liwia* (b) as sister taxon to *Naraoia*. Numbers refer to derived characters as follow: 1. trunk narrowed anteriorly relative to head shield, widest posteriorly; 2. lack of dorsal eyes; 3. pygidium longer than head shield; 4. trunk fused as single tergite; 5. laterally deflected antennules; 6. large, ramifying anterior pair of gut diverticula; 7. bloated, mud-filled gut; 8. very wide doublure; 9. median keel on pygidium.

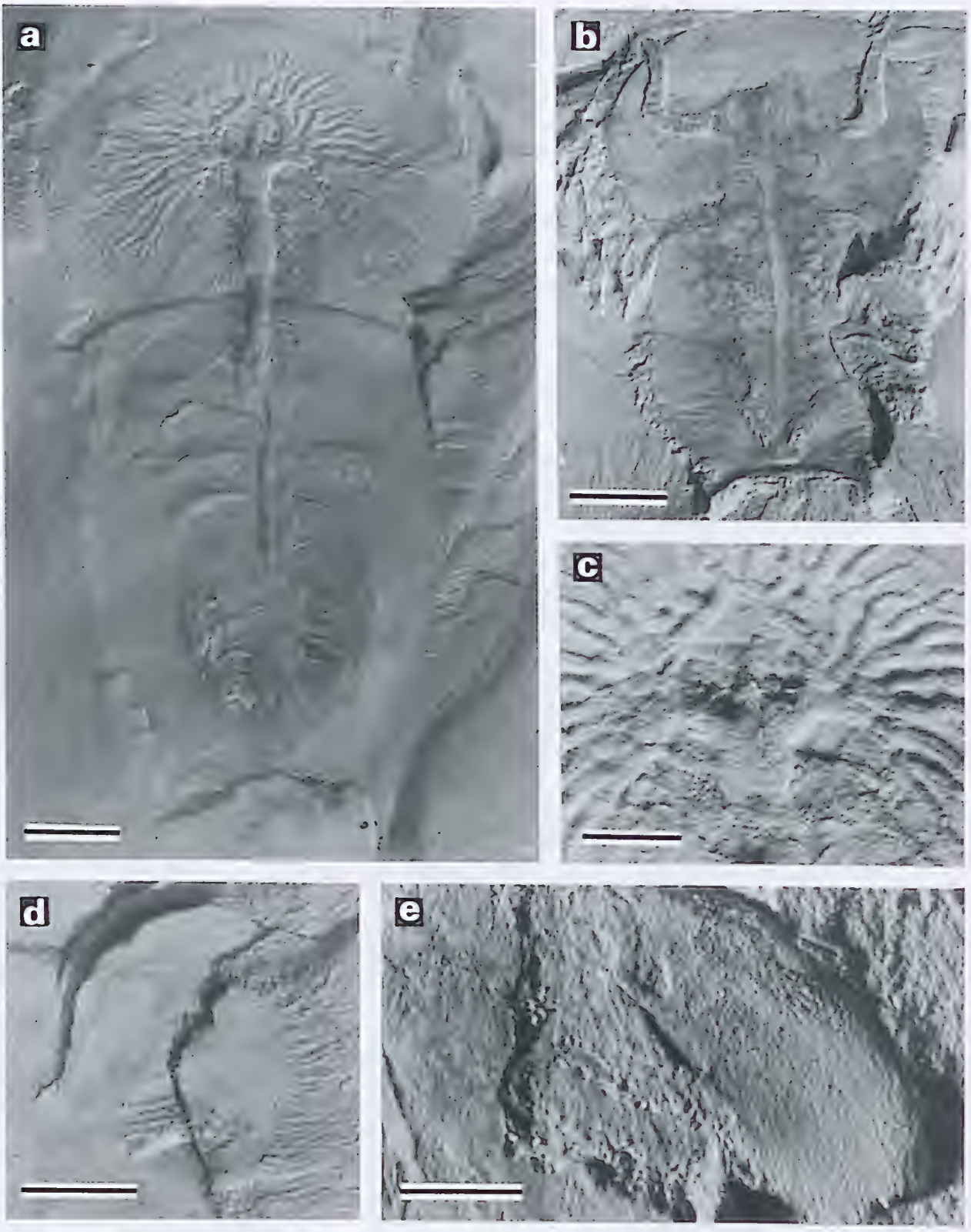

Fig. 16. *Naraoia spinosa* Zhang & Hou, 1985. a, c, d, ELRC 16182b, from locality MQA (see Fig. 17 for camera lucida drawing). a, dorsal view of large individual. Note that right antennule is recurved anteriorly distal to the head shield, but is oriented laterally from its attachment point. Light from NW. Scale bar 4 mm; c, detail of cephalon, showing foregut and proximal parts of anterior diverticula. Light from NW. Scale bar 2 mm; d, detail of distal parts of anterior two trunk exopods. Light from NW. Scale bar 2 mm. b, ELRC 16074a, from locality MW2, dorsal view of complete specimen with head shield excavated to expose antennules. Light from NW. Scale bar 5 mm; e, ELRC 16070, dorsal view of distal lobe of trunk exopod. Light from W. Scale bar 2 mm.

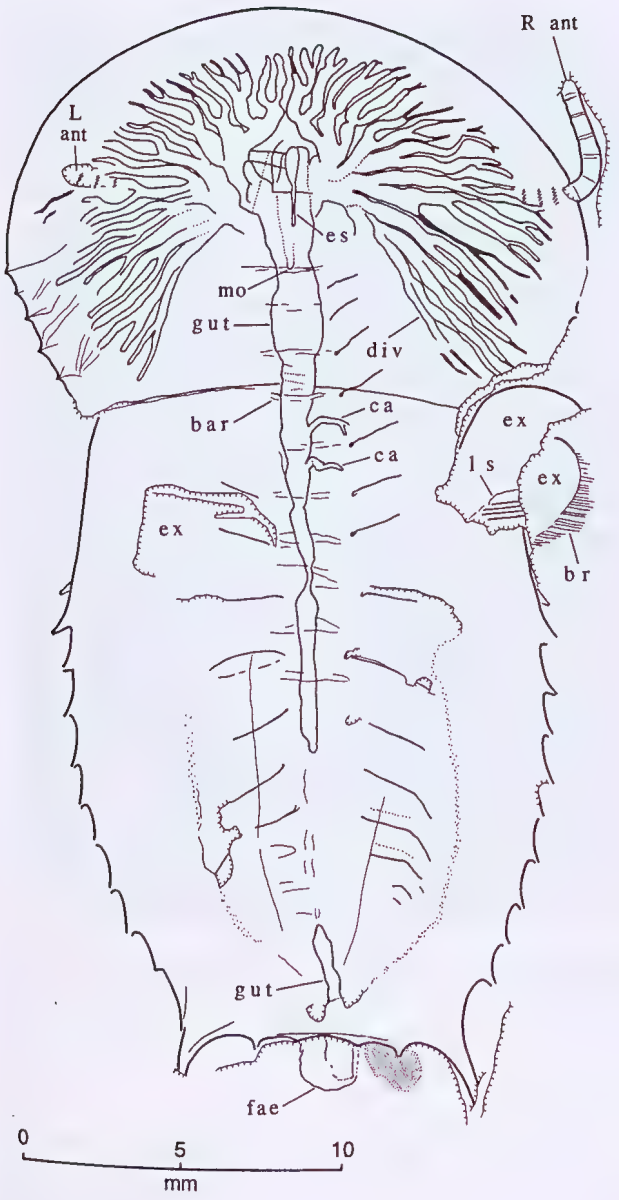

Fig. 17. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 16182b (see Fig. 16a,c,d). See Appendix for abbreviations.

New information on the ontogeny of naraoiid appendages is available from *Naraoia spinosa* (Figs 22, 23). This may provide another source of data for evaluating relationships within Naraoiidae and between naraoiids and other groups. Post-antennular appendages of juveniles have short, non-imbricate setae splaying from the slender shaft of the exopod, as well as splaying distally from the tip of the exopod. The typical arachnate imbrication of the lamellar setae is attained later in ontogeny, and we accordingly regard the state shown by juveniles of *N. spinosa* as a plesiomorphy. Juvenile naraoiid morphology shows a closer approximation to exopod structure in *Agnostus pisiformis* than has been detected in other taxa at more advanced stages of ontogeny. In some instances, these similarities are detailed. For example, the first post-antennular cephalic limb of *Agnostus* (Müller & Walossek, 1987: fig. 6B) and the antennule of *Naraoia spinosa* (Fig. 22a) possess very similar configurations of setae. The comparable region is situated distally on the second appendage in *Agnostus* but may extend farther proximally on the antennule of *Naraoia*. In both taxa, a short seta is developed on the posteromedial edge of each podomere on its anterior margin, whereas a pair of long setae is present on the posterior edge of the podomeres. Given the lack of evidence for an especially close relationship between agnostids and naraoiids, this arrangement in juvenile morphology is evidently a deeply nested character. The antennule of *Agnostus* appears to be serially homologous with the sole ramus of the following limb, i.e., the antennal exopod (both bearing stiffened setae on similarly shaped podomeres). Cisne (1981: 130) made essentially the same conjecture, that the trilobite antennule is the serial homologue of the post-antennular exopod shaft. The inferred serial homology of the antennule and the antennal exopod in *Agnostus* provides an explanation for the similarity of the the antennule of *Naraoia spinosa* to the antenna of *Agnostus*. It is thus not surprising that the antennule of juvenile *Naraoia* bears setae similar to those on all post-antennular exopods. Müller & Walossek (1987: 35) observed that the structure of the setose exopod of the antenna of *Agnostus* resembles the swimming limbs of crustacean larvae. Accordingly a locomotory function might be ascribed to the setose antennule of juvenile *Naraoia*, which assumes a predominantly sensorial function later in ontogeny.

Ecological disparity

Inferences about life habits can be made from the anatomical differences between *Naraoia* and *Misszhouia*. This morphological disparity is consistent with differences in the manner of preservation of the two taxa. On both counts (morphology and preservational style), *Naraoia spinosa* may be identified as a deposit feeder.

The two naraoiids in the Chengjiang fauna possess markedly different digestive systems. *Misszhouia longicaudata* shows a relatively simple gut, with small, segmentally set caeca that ramify close to the gut. The gut is narrow, not wider than the sternites (Figs 2a, 13c, 18a), about 7–8% of the exoskeletal width. In contrast, the gut in *Naraoia spinosa* is equipped with a complex system of ramifying diverticula that fills much of the cephalon, leaving only a narrow margin free of the diverticula. The gut itself is 14–18% of the exoskeletal width, twice as wide as in *M. longicaudata*. The thickness of the mudfill indicates that prior to compaction, the gut in both species was circular in section. The gut in *N. spinosa*, when filled, thus held a volume four to five times that of *M. longicaudata*, and even more when the caeca are included.

A very large, complex system of gut diverticula and a gut with great holding capacity indicate that the diet

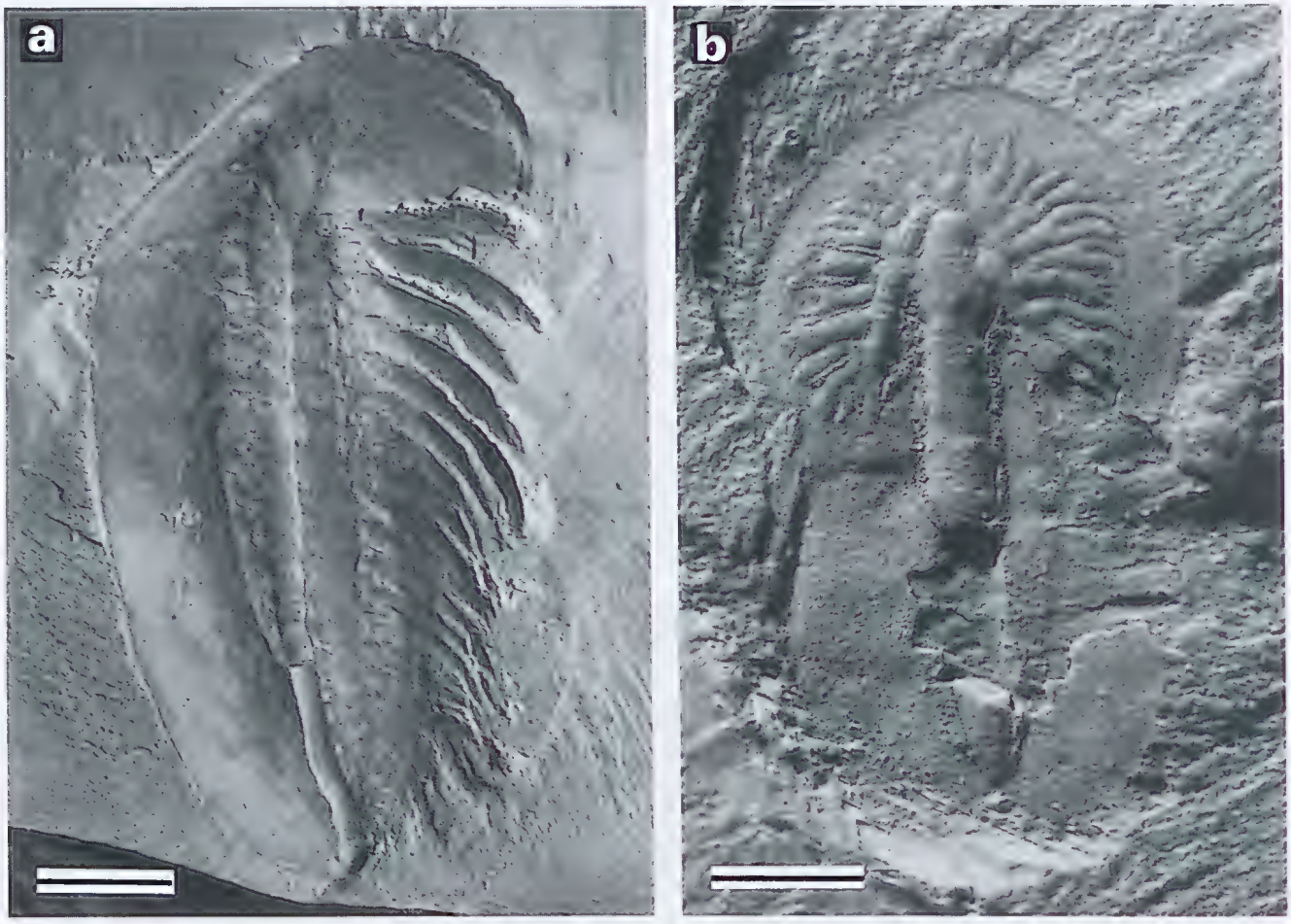

Fig. 18. a, *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11686a, specimen in dorsolateral view. Light from W. Scale bar 5 mm; b, *Naraoia spinosa* Zhang & Hou, 1985. ELRC 12131a, from locality MN4 (see Fig. 19 for camera lucida drawing). Small individual showing mud-filled gut and diverticula. Scale bar 1 mm.

of *Naraoia spinosa* was low in nutrition. The majority of *N. spinosa* specimens are preserved with the digestive system filled with sediment indistinguishable from the surrounding matrix. The frequency of mudfill of the gut and mud-packed diverticula in the cephalon provide strong evidence that sediment ingestion was the typical feeding mode of *N. spinosa*, and we conclude that it was a deposit feeder.

A deposit feeding mode of life for *Naraoia spinosa* agrees well with other aspects of its morphology. Its antennules are directed laterally, not anteriorly where they would both hinder the cephalon ploughing or digging into the mud, and risk damage during such activity. Another feature apparently adapted for this life style is the shape of the exopods. These do not have slender distal lobes and huge fans of setae comparable to those in *Misszhouia longicaudata*. Instead, at least the anterior trunk limbs have exopods with large, paddle-shaped distal lobes and short lamellar setae on the shaft (Figs 16d,e, 17), a morphology well suited for digging into soft sediment.

The mode of life outlined here for *Naraoia spinosa* is also suggested by the attitudes in which the specimens are preserved. The cephalon is usually preserved at an angle to the bedding plane, and is quite commonly directed nearly vertical into the sediment (Fig. 20a). Also the trunk is usully preserved at an angle to the plane of bedding (Fig. 20b), and the angle between the head and trunk has a mode between 80 and 100 degrees, with some specimens folded through 120–130 degrees (Fig. 21). It is not known whether these attitudes are the result of struggle during entombment or if individuals are preserved *in situ*.

Misszhouia longicaudata lacks the features indicating deposit feeding in *Naraoia spinosa*. The anteriorly directed antennules would have hindered ploughing in the sediment, and the delicate exopods would be unsuitable for digging. The large, imbricating exopod fans could conceivably be difficult to free from mud, and whatever their function (respiration, swimming, or other), that function would hardly have benefitted from a mud cover. In *M. longicaudata*, the gut is only rarely mud-filled, and we interpret these instances as the result of mud ingestion during death struggle, parallelled in many other animals in the Chengjiang fauna. Specimens of *M. longicaudata* display less declination of the head and

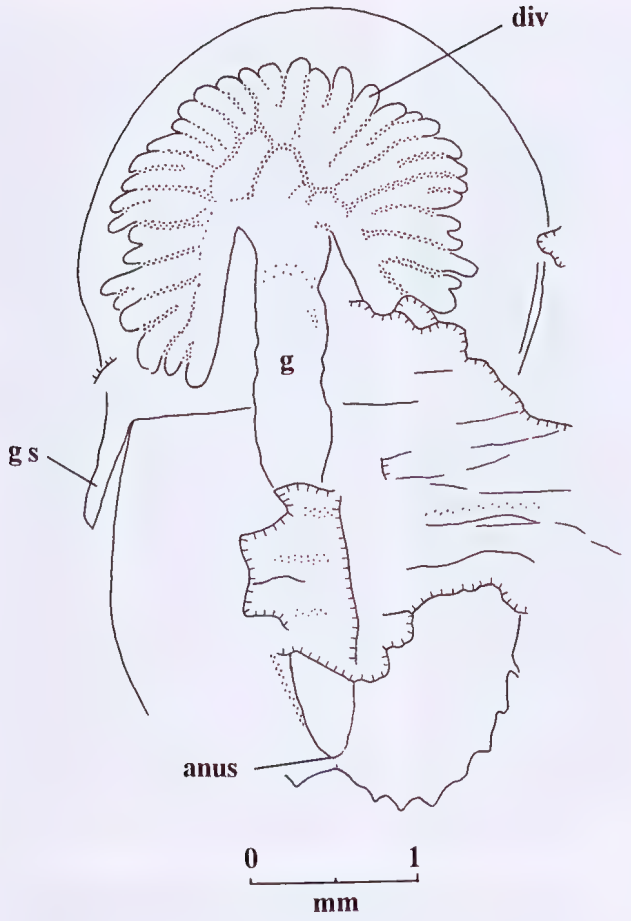

Fig. 19. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 12131a (see Fig. 18b). See Appendix for abbreviations.

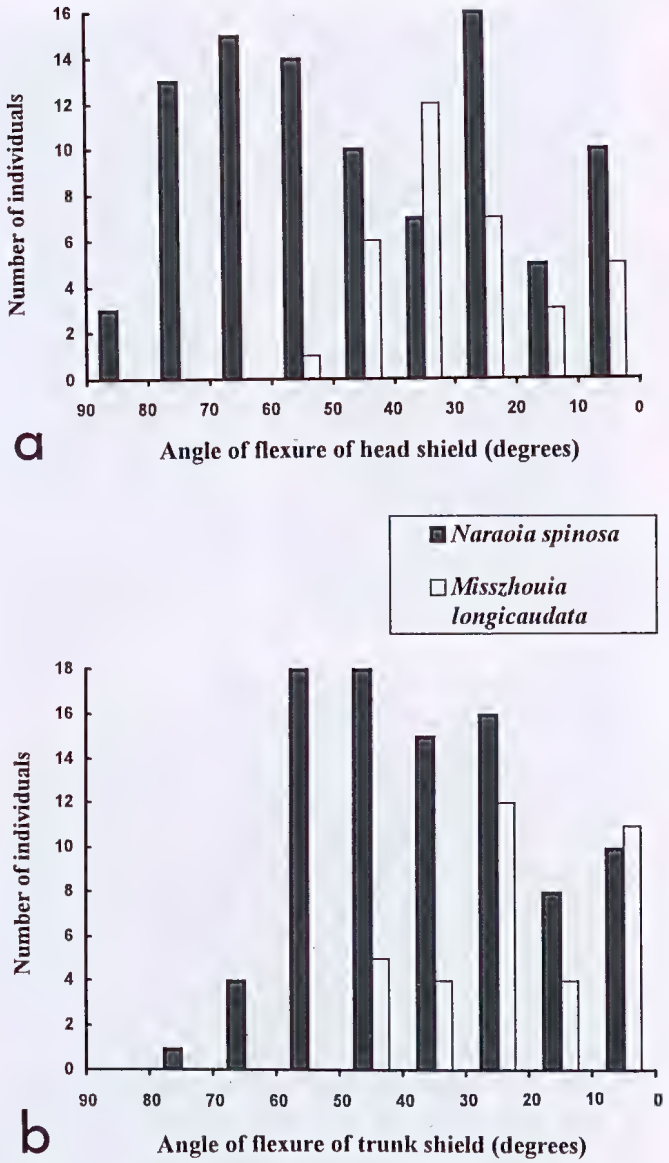

Fig. 20. Histogram depicting angle of flexure of head shield (a) and trunk shield (b), measured from horizontal bed surface, for *Naraoia spinosa* (N=93 and 90 for Figs a and b, respectively) and *Misszhouia longicaudata* (N=34 and 36 for Figs a and b, respectively) from the Chengjiang fauna.

trunk shields into the sediment than is the case for *Naraoia spinosa* (Figs 20, 21).

The large, spinose endite on the basis in *Misszhouia* resembles the condition in trilobites and other arthropods that have been interpreted as predators and/or scavengers, and we regard these habits as probable for *M. longicaudata*. Whittington (1977) interpreted *Naraoia compacta* as a predator and scavenger based primarily on the size of the gnathobase on the basis and the spinose endite on the first podomere of the endopod. He disputed the possibility that deposit feeding was a major part of its habits (1977: 438). As discussed above, we cannot uphold this claim with respect to the closely allied *N. spinosa*.

Naraoia compacta and *N. spinosa* share most features interpreted here to indicate deposit feeding. Such features present in both species are the extensive gut diverticula in the cephalon, the high holding capacity of the gut, and the laterally directed antennules. As in *N. spinosa*, the gut in *N. compacta* is often preserved filled with mud. Whittington (1977: figs 66, 67) documented specimens of *Naraoia compacta* with the head and trunk shield flexed at right angles. As detailed above, flexure

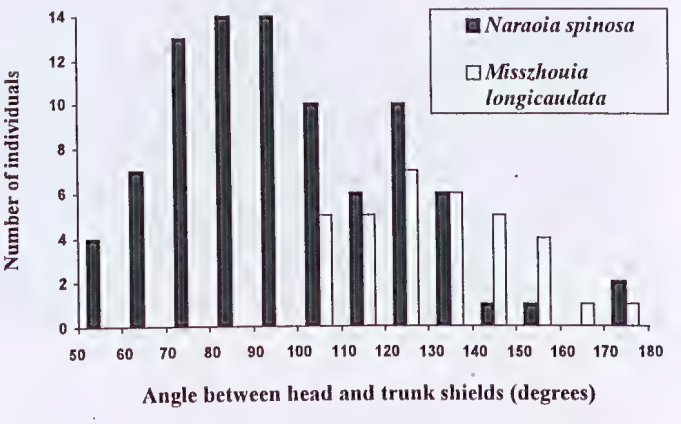

Fig. 21. Histogram depicting angle between head and trunk shields for *Naraoia spinosa* (N=88) and *Misszhouia longicaudata* (N=34).

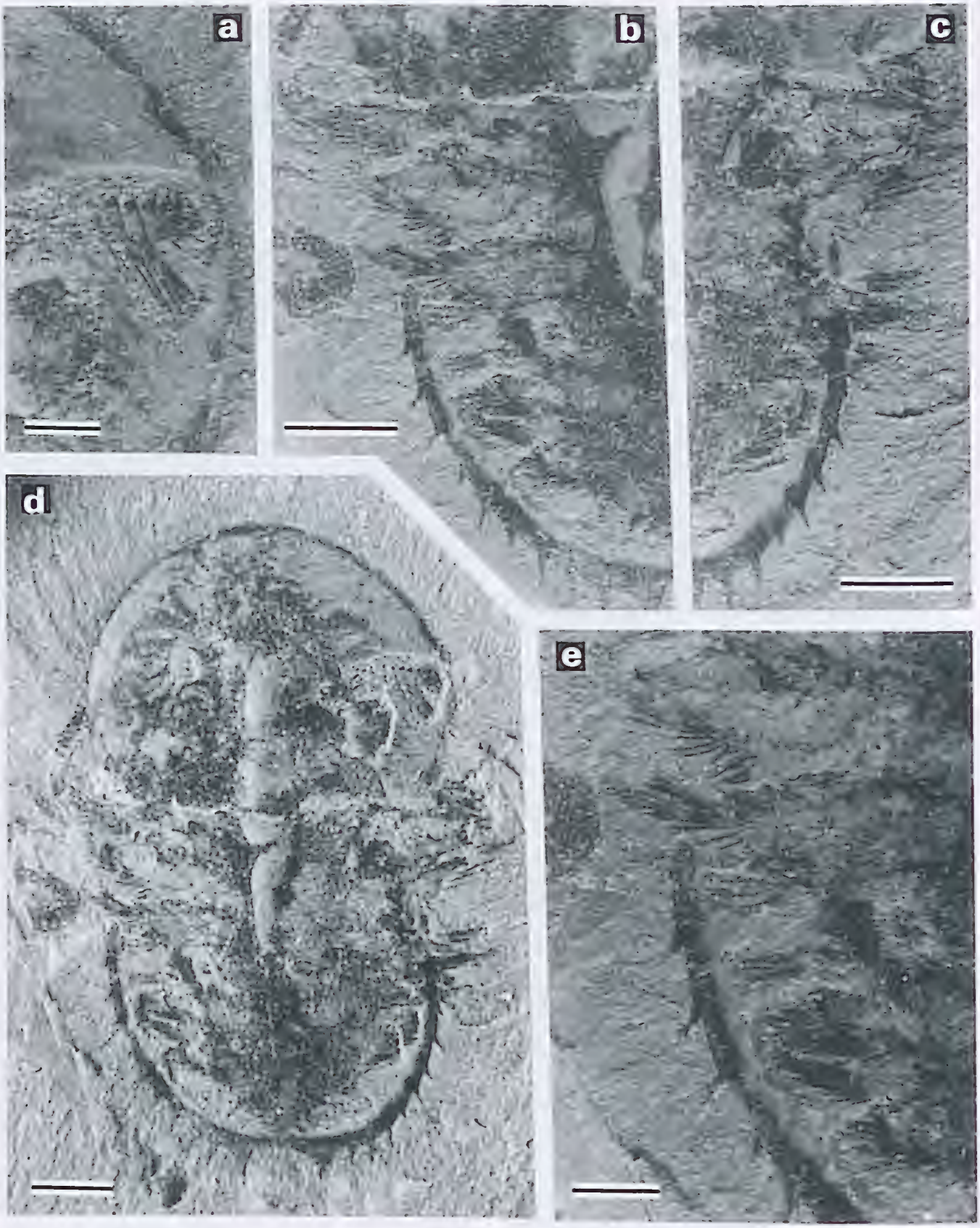

Fig. 22. *Naraoia spinosa* Zhang & Hou, 1985. Juvenile specimen ELRC 10983, from locality MN5 (see Fig. 23 for camera lucida drawing). All dorsal views, high light from S except Fig. d, high light from W. a, detail of right antennule. Note short setae on anterior edge of antennomeres, long paired setae on posterior edge of antennomeres. Scale bar 0.5 mm; b, left side of specimen. Scale bar 1 mm; c, right side of specimen. Scale bar 1 mm; d, complete specimen. Scale bar 2 mm; e, detail of left side of trunk. Scale bar 0.5 mm.

at the head/trunk juncture is also the common preservational mode for *N. spinosa*. The only significant anatomical difference between the two species of *Naraoia* appears to be the limb structure in *N. compacta*, characterised by more slender distal lobes of the exopods (but stouter than in *Misszhouia longicaudata*). However, it should be noted that the limbs in *N. spinosa* are still largely unstudied, and that the complete shape of the exopod fan and the presence of endites in that species are unknown. The failure of specimens of *N. spinosa* to part along a large exopodal surface (as is the case for *Misszhouia*) indicates that the exopod fan of *N. spinosa* is of smaller area than in *N. compacta*.

Whittington's (1977) interpretation of feeding habits of *Naraoia compacta* is based mainly on the large gnathobases. The large, undivided posterior shield was regarded as another adaptation for capturing soft prey (by providing an expansive area for muscle attachments), but this feature may be typical for a broader group of naraoiids (Fig. 15a). We consider that several features indicate deposit feeding for *N. compacta*, and that the only feature possibly indicating predation—the spinose endites—is unknown in *N. spinosa*. We might, however, infer its presence also in that species, given the broader distribution of this state in basal trilobites (Ramsköld & Edgecombe, 1996). A detailed investigation of feeding habits of naraoiids is beyond the scope of this contribution, but the discussion presented here at least indicates that the mode of life of naraoiids is more varied than previously thought.

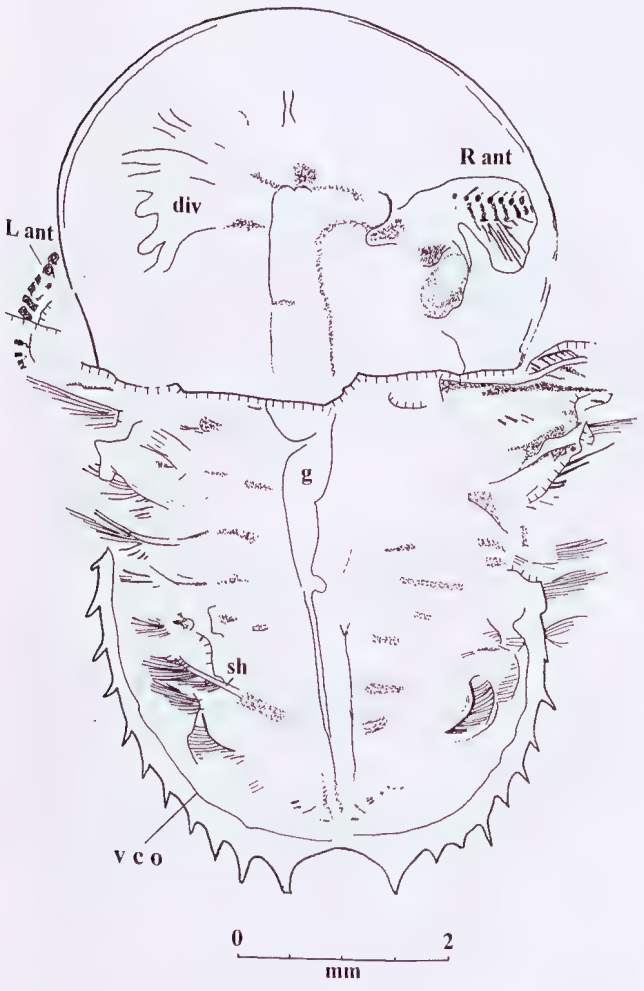

Fig. 23. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 10983 (see Fig. 22). See Appendix for abbreviations.

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Appendix 1

Abbreviations used in Figures

a e	anterior edge of trunk shield
a m	arthrodial membrane
ant	antennule
ba	basis
bar	transverse tendinous bar
br	bristles on distal lobe of exopod
C2–C4	cephalic limbs 2–4
ca	caecum
div	anterior gut diverticulum
d l	distal lobe of exopod
es	esophagus
en	endopod
ex	exopod
fae	faeces outside gut
f o	frontal organ
g	gut
gl	digestive gland
g s	genal spine
h	ovate lobe of hypostomal complex
h s	head shield
L	left
l s	lamellar setae of exopod
m f o	median frontal organ
mo	mouth
p ar	proximal articulation of basis
p e	posterior edge of head shield
R	right
sh	shaft of exopod
T1	first (anteriormost) trunk limb
v c	ventral cuticle
v c i	inner margin of ventral cuticle
v c o	outer margin of ventral cuticle

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A Tetrapod Fauna from the Permian of the Sydney Basin

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ABSTRACT. A recent discovery by Bruce Ross of Oceanic Coal Australia Ltd in the roof of the Borehole Seam, West Wallsend Colliery, is the first well documented evidence of a tetrapod fauna from the Permian of Australia. The Borehole Seam (Newcastle Coal Measures, Lambton Subgroup) lies immediately above the Waratah Sandstone which forms the base of the Newcastle Coal Measures and is most likely Kazanian in age. Preliminary study has shown that among the five tetrapod specimens recovered at least temnospondyl amphibians are represented. The only previous tetrapod body fossil from the Australian Permian is a temnospondyl amphibian, *Bothriceps major*, from Airly, to the north-west of Sydney. Tetrapod trace fossils have been known for some time in the southern part of the Sydney Basin where the Illawarra Coal Measures have yielded several sets of reptilian footprints. Tetrapods were therefore living to the north, west and south of the Sydney Basin in the Late Permian of Australia.

WARREN, ANNE, 1997. A tetrapod fauna from the Permian of the Sydney Basin. Records of the Australian Museum 49(1): 25–33.

In Australia, records of tetrapod body fossils date from the Late Devonian Cloghnan Shale near Forbes, New South Wales (Campbell & Bell, 1977) and Devonian tetrapod footprints have been described from the Genoa River beds of northern Victoria (Warren & Wakefield, 1972). Most recently the first Early Carboniferous tetrapod fauna from the Southern Hemisphere has been found in Queensland (Thulborn *et al.*, 1996). Australia also has a widespread and diverse Early Triassic temnospondyl fauna, especially in the Arcadia Formation of Queensland (Warren, 1991) which is remarkable for the rarity of therapsid reptiles. It is surprising therefore that only a single tetrapod, an amphibian from near the Permo-Triassic boundary of the Sydney Basin (Woodward, 1909), has been recovered from the period between the Early Carboniferous and the Early Triassic. This time interval is important for the emergence of the therapsids which are present in quantity in other continents, especially in the Permian.

The recent discovery of a tetrapod fauna from well below the Permo-Triassic boundary in the Sydney Basin is significant as a first step to filling in this gap. The find was made by Bruce Ross, of Oceanic Coal Australia Ltd, who had previous experience collecting Palaeozoic tetrapods with the legendary Stan Wood of Scotland. Although the state of preservation of the fossils prevents their detailed description and precise identification, the fact that a tetrapod fauna was present is of significance. In this paper I have taken the opportunity to summarise our knowledge of both body and trace fossils from the

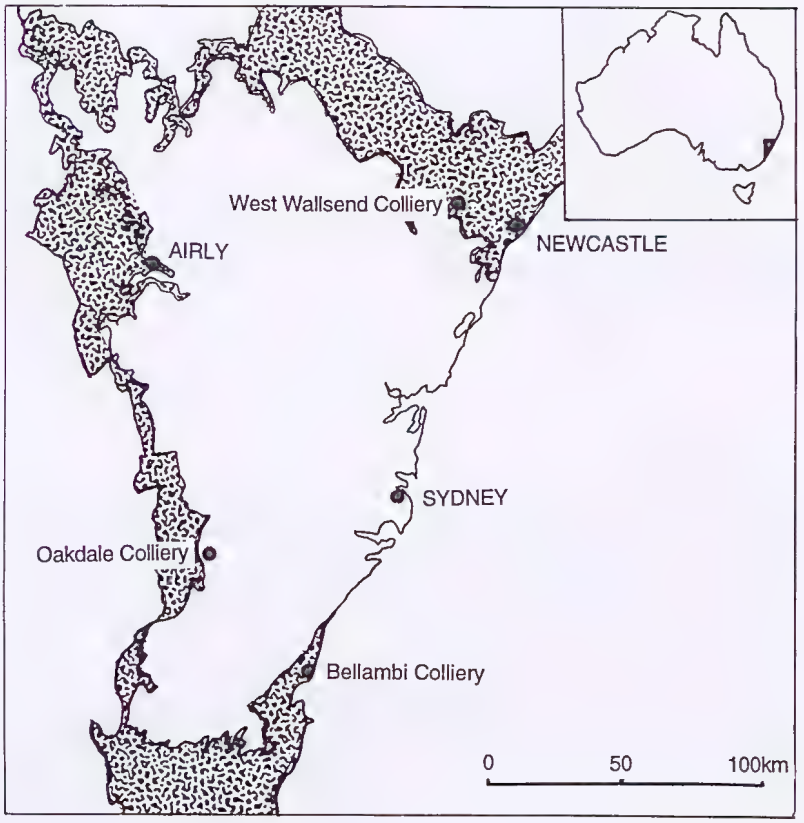

Fig. 1. Map of the central part of the Sydney Basin showing the tetrapod fossil localities in relation to Sydney and Newcastle. Permian outcrop is shaded.

Permian of the Sydney Basin as well as to describe the new finds. A map of the fossil localities is presented in Figure 1 and a chart of their temporal relationships is presented in Figure 2.

		Northern Sydney Basin	Southern & Western Sydney Basin
Early Triassic	Scythian	NARRABEEN GROUP	NARRABEEN GROUP
		?	?
Late Permian	Tatarian	NEWCASTLE COAL MEASURES	***BULLI COAL***
		BOREHOLE SEAM	ILLAWARRA COAL MEASURES
	Kazanian	TOMAGO COAL MEASURES	**GLEN DAVIS FMN**
			ILLAWARRA COAL MEASURES

Fig. 2. Stratigraphic relationships between the tetrapod-bearing strata which are shown in bold type. The new West Wallsend fauna is from the Borehole Seam, the temnospondyl *Bothriceps major* from the Glen Davis Formation, and both sets of footprints from the Bulli Coal.

Tetrapod body fossils

Bothriceps australis Huxley, 1859—BM(NH) R23110

According to Watson (1956) this specimen was bought by the British Museum in 1948 from a person of whom nothing is known and was said to have been found in "Australia". Watson considered that the structure of *Bothriceps australis* suggested that it was as early as, or earlier than, *Bothriceps major* (discussed below) and subsequent authors have followed Watson in assigning it a Late Permian age. The evidence for this conclusion is tenuous and an Early Triassic age is more likely than Permian. The specimen shows several grade characters common to Mesozoic temnospondyls, such as the loss of the supraoccipital, basioccipital and opisthotic from the occiput, and the presence of a firm suture between the pterygoid and the parasphenoid.

Stratigraphic position. Unknown. A label associated with the specimen says it is from the "Hawkesbury Beds (Permian)". This was probably an educated guess but could well be correct except that the Hawkesbury Sandstone of the Sydney Basin is now early Middle Triassic.

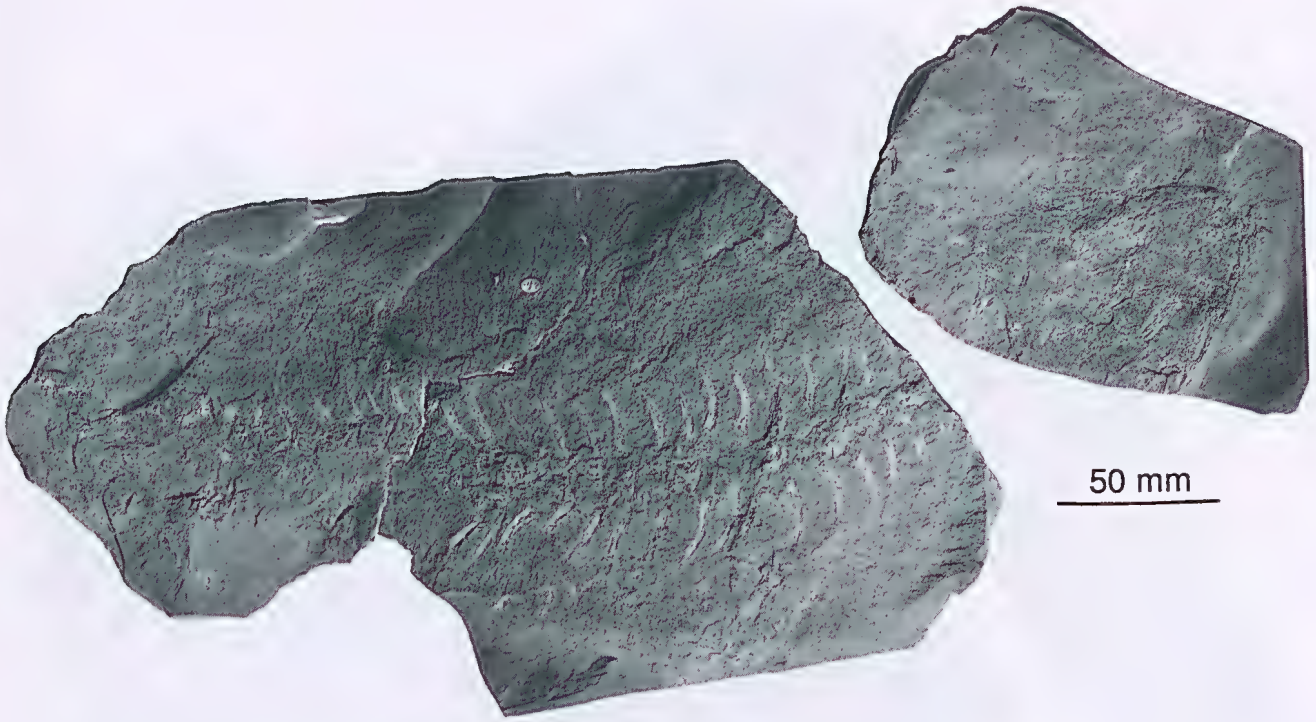

Fig. 3. The temnospondyl amphibian *Bothriceps major*; head MMF12697a, body AM F50977.

Bothriceps major Woodward, 1909

This specimen (Fig. 3) which was recovered from the Commonwealth Oil Corporation's shale mine at Airly, near Capertee in the west of the Sydney Basin is preserved in three pieces distributed in three different repositories as follows: head, Geological Survey of New South Wales, Sydney, MMF 12697a; body, Australian Museum, Sydney, AM F 50977; counterpart head and body, Natural History Museum, London, BM(NH) R3728.

Woodward (1909) recognised the specimen as a brachyopid amphibian, placing it in the same genus as *B. australis*, presumably because they were both Australian, but decided to separate it specifically because of a difference in the size of its orbits, those of *B. major* being relatively smaller.

Watson (1956) transferred the specimen to a new genus, *Trucheosaurus*, largely because " in the few structures clearly shown in the only known specimen it differs from the type of the genus *Bothriceps* and indeed from all other known genera of the family" and also because "the specimen is important as showing the occurrence of a typical brachyopid at an early horizon". The name *Trucheosaurus*, from the Greek for rags and tatters, reflects Watson's opinion of the state of preservation of the specimen. It was returned to *Bothriceps* by Welles and Estes (1969). All three blocks of *B. major* are currently being restudied by Dr C. A. Marsicano and myself; we intend removing *B. major* from the family Brachyopidae.

Stratigraphic position. The torbanite from which *B. major* originated is in the Glen Davis Formation of the Charbon Subgroup, a lower deltaic facies of the Late Permian Illawarra Coal Measures (Eui Kyoo Yoo pers. com., 1995). Palynological evidence indicates that the Glen Davis Formation is older than Tatarian but not older than Kazanian (McMinn, 1985; Foster pers. com., 1995). Thus *B. major* is indeed Permian and stratigraphically the earliest recorded member of the stereospondyl radiation.

New material from West Wallsend

A rock fall in 1984 from the roof of the Borehole Seam at the West Wallsend Colliery owned by Oceanic Coal Australia Ltd. was recognised by mining engineer, Bruce Ross, as containing fossil vertebrates. These are preserved in concretions within a highly carbonaceous shale and have been dorsoventrally compressed and partially metamorphosed so that little detail of their anatomy remains. All appear to have been split through the centre of the specimen so that none present a dorsal or ventral aspect. While the majority of the specimens are fish, as indicated by the presence of lepidotrichia and scales, four concretions appear to contain tetrapod remains.

AM F95421, AM F95122. These specimens (Figs 4, 5) are part and counterpart of a boomerang shaped concretion which contains most of a tetrapod vertebral column with attached ribs. It is possible to count

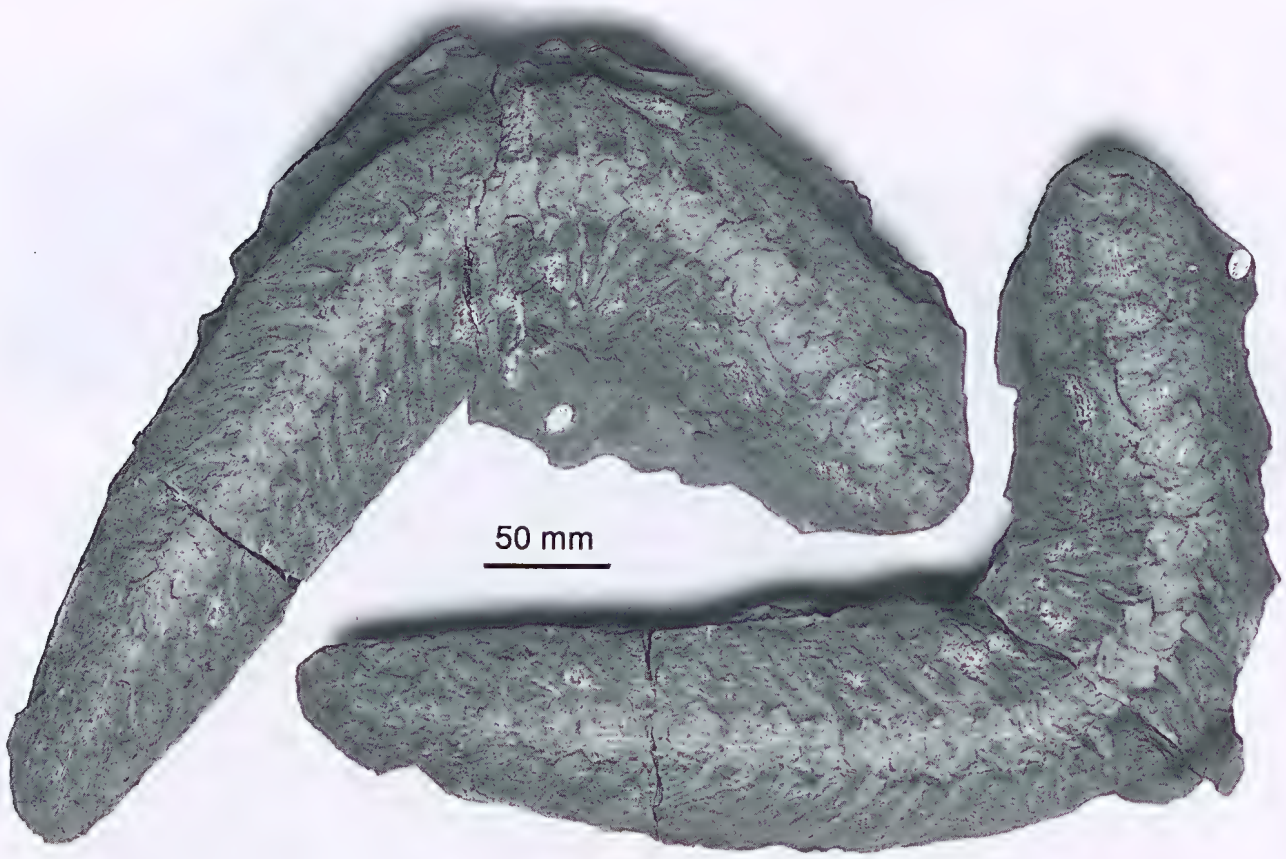

Fig. 4. Temnospondyl vertebral column from West Wallsend: AM F95421, AM F95422.

approximately 24 presacral vertebrae and about ten caudals. A count of between 23 and 26 is typical of the few temnospondyls in which an articulated column is preserved and a similar range is found in early reptiles (Romer, 1956).

Anteriorly the column is twisted so that neural arches are visible as well as ribs. Here several vertebrae appear typically rhachitomous; neural arches articulate with large pleurocentra separated by smaller intercentra. Posterior to the eighth neural spine the column twists so that it is seen in frontal section, with symmetrically arranged ribs. At centrum twenty four the column again twists revealing two neural arches in the same section as ribs. This part of the column may be immediately postsacral; tetrapods typically have a postsacral area which is rib bearing before the haemal arches begin and the ribs are lost. The final two centra preserved appear to bear haemal arches as well as neural arches.

Beneath vertebrae five and six three bones may be parts of the anterior limb or they could be expanded pectoral ribs.

This specimen appears to be a temnospondyl amphibian as evidenced by the rhachitomous appearance of several of its more anterior vertebrae.

AM F97240 (Fig. 6A). Unfortunately the counterpart of this small concretion was not recovered. An articulated but buckled section of vertebral column is represented by approximately fifteen centra at least five of which are associated with ribs. It is not possible to tell whether these represent rhachitomous or stereospondylous centra, or whether they are from temnospondyls or amniotes.

AM F97241 (Figs 6B, 7). Potentially the most complete of the collection, this specimen, which is preserved in part and counterpart, includes what appear to be cranial and mandibular remains as well as centra, ribs, and possible skin impressions.

A single tooth associated with the mandible is longitudinally infolded in its lower half indicating probable temnospondyl affinity. Although the bones associated with this tooth together define the shape of a mandible none can be positively identified as individual mandibular elements.

Some of the presumed cranial bones are ornamented, with fine ridges radiating from the centres of ossification. No midline symmetry can be found among these elements and none can be named. Individual bones are larger than expected if they are considered to belong to a skull associated with the

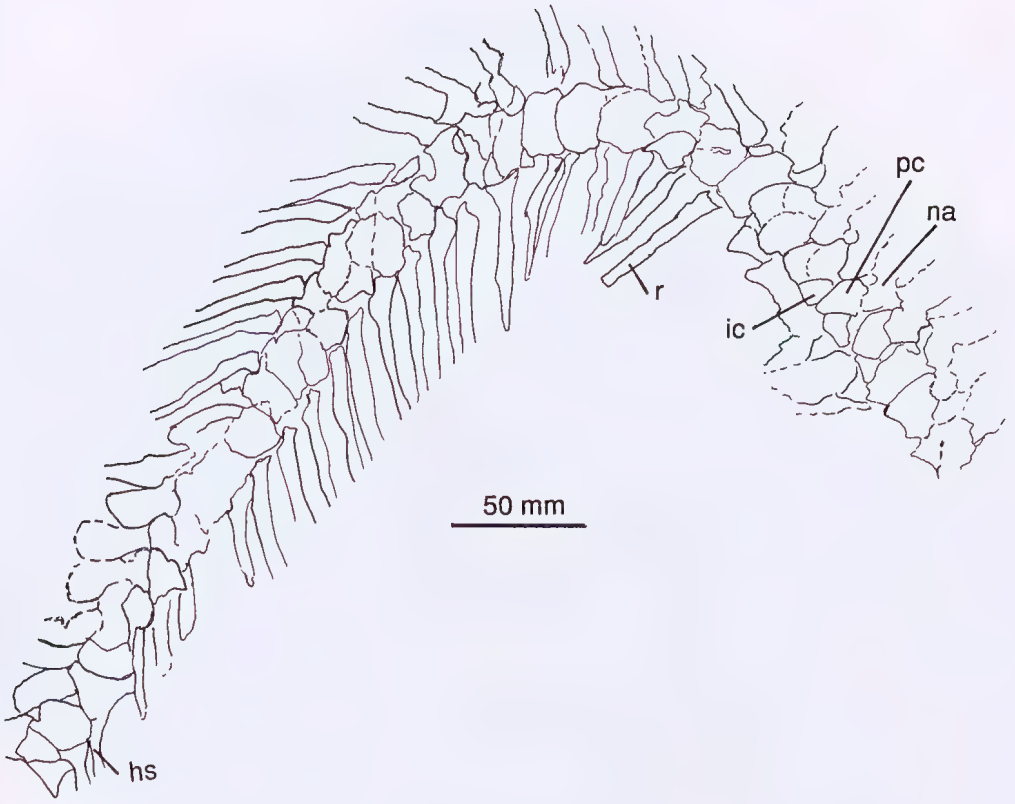

Fig. 5. Outline of bones of temnospondyl vertebral column AM F95421. Abbreviations used in this and subsequent figures are as follows: c—centrum, hs—haemal spine, ic—intercentrum, l—limb element, m—mandible, pc—pleurocentrum, r—rib, s—?skin impression, t—tooth.

mandible and together they occupy too large an area for such a skull. Therefore it is likely that elements of the pectoral girdle are also present.

The two vertebral centra associated with AM F97241 could be rhachitomous or stereospondylous.

Dimpled areas of sediment (Fig. 7) adjacent to the bone in this and AM F97243 may be impressions of soft body parts but equally could be cleavage patterning. They are not present elsewhere on the block of sediment or in the other specimens. Their indentations are too irregular in arrangement to be marks left by small scales and they may be skin impressions.

This specimen is identified as most likely to be a temnospondyl amphibian on the basis of its infolded teeth. Some fish, notably some sarcopterygians, shared folded teeth with early tetrapods, but the last known of these was *Ectosteorachis* from the Early Permian. Rarely, actinopterygians may have folded teeth. The absence of lepidotrichia or fish-like scales associated with the specimen suggests that it is not an actinopterygian, and the vertebral centra are rather large and heavily ossified for a fish.

AM F97242 (Fig. 6C). While this concretion did not split cleanly through the specimen, so that it is fragmented into five main blocks, the colour differentiation is better. Possible cranial material, vertebrae, ribs and limb elements are present. The cranial segment is traversed by a groove which could be a sensory canal and has a raised area which may be a centre of ossification adjacent to the groove. Two slightly curved lateral margins could be the posterolateral borders of interpterygoid vacuities if the element is a parasphenoid. On the other hand they could define the stem of an interclavicle!

The centra look more reptilian than amphibian, being spool-shaped with one or both ends concave as some sections are solid and others bear a central perforation of varying diameter. Mesozoic temnospondyls sometimes have such centra but Palaeozoic temnospondyls do not, and reptiliomorph amphibians, which do have spool-shaped centra, have not been found in the Southern Hemisphere.

All limb remains, except one, have flattened rather than rounded ends and could be temnospondyl or reptile.

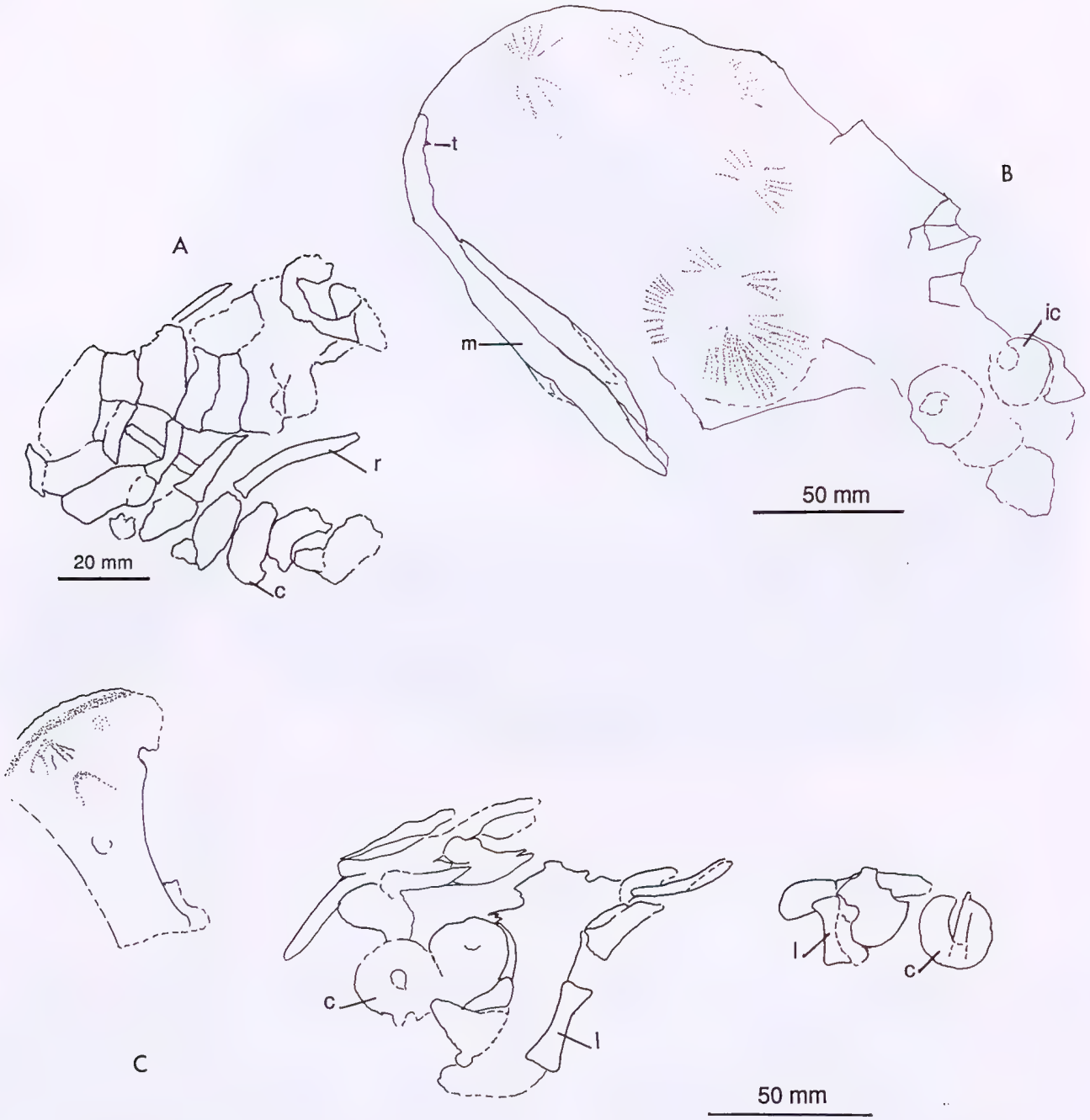

Fig. 6. Outline drawings of bones discernible on **A**—AM F97240, tetrapod vertebral column; **B**—AM F97241, ? temnospondyl remains; **C**—AM F97242, tetrapod ? cranial (left) and postcranial (centre and right) elements. In B the tooth is transposed from the counterpart. Photographs of specimens A and C are not provided as too little colour differentiation exists between bone and sediment. The three areas of bone depicted in C are shown in their natural relationship.

Their size indicates that they are distal limb elements or metapodials.

AM F97243. All remains on this fragmented block are carbonised and difficult to differentiate from the matrix. It appears to be a partial articulated vertebral column with associated ribs.

Stratigraphic position. The Borehole Seam is the lowermost part of the Lambton Subgroup and lies immediately above the Waratah Sandstone which forms the base of the Newcastle Coal Measures in the Newcastle area (McMinn, 1985). The Borehole Seam is Kazanian in age (Diessel, 1980). On McMinn's palynostratigraphic correlation of the Upper Permian of the Sydney Basin (1985, fig. 3) it is a little younger than the Glen Davis Formation from which the temnospondyl, *Bothriceps major*, was recovered.

Fig. 7. Photograph of AM F97241, ? temnospondyl remains.

Footprints

Bellambi Colliery

The Bellambi track was discovered following a rock fall from the roof of the Bulli Seam in 1913. It was identified by Dun, who was paleontologist to the New South Wales Geological Survey at the time, as comparable to the reptilian footprints described as *Ichnium gampsodactylum* found in Permian rocks in Germany and the English midlands, and was illustrated by Harper (1915, Plate XXIV) and Herbert & Helby (1980, p. 116). A formal description of these tracks as an ichnotaxon, *Dicynodontipus bellambiensis*, has now appeared (Retallack, 1996). They are argued to have been made by a dicynodont, most likely *Lystrosaurus*, but part of the evidence for this generic identification rests on Retallack's acceptance of a Triassic age for the trackway (see below).

Oakdale Colliery

A second tetrapod trackway (AM F97129, Fig. 8), also from the roof of the Bulli Seam, but this time from the Oakdale Colliery, was donated to the Australian Museum in 1995 by A. Wright. Like the Bellambi track, the Oakdale specimen has a five digit manus with a five digit pes and is therefore also reptilian in origin. The tapered digits suggest claws were present, thus reinforcing the identification of the trackmaker as reptilian. The prints are considerably smaller than those from Bellambi but otherwise are similar in having fore and hind prints of equal size with equally expressed digits. A greater pace angulation and a slightly more digitigrade stance indicate that, although the tracks were made by a similar but smaller animal to the one at Bellambi, it was moving at a faster pace. A small dicynodont or procolophonid are most likely to have made the tracks, although tracks attributed to procolophonids (Haubold, 1971) do not have claw marks.

Fig. 8. Amniote trackway (natural mould) from the Oakdale Colliery. AM F97129.

Both the Bellambi and Oakdale footprints are associated with arthropod tracks.

Stratigraphic position. In the southern part of the Sydney Basin, near Wollongong, the Coal Cliff Sandstone, which preserved both the Bellambi and Oakdale trackways, is the lowermost unit of the Narrabeen Group. The Coal Cliff sandstone forms the roof of the Bulli Seam and thus marks the top of the Illawarra Coal Measures (Bowman, 1980), a stratigraphic position close to the Permo-Triassic boundary. The exact position of this boundary in the Sydney Basin is debatable. Palynological evidence indicates that the Narrabeen Group, which overlies the coal measures, extends downwards into the Permian (Retallack, 1980; Archbold & Dickens, 1996) and that the trackways were made before the Late Tatarian. On the other hand, Retallack (1996) argued that the facies change from coal measures to alluvial shales and sandstones at the base of the Narrabeen Group marks the Permo-Triassic boundary. He additionally cites a lightening of the 13 C isotopic ratio of kerogen in sediments at the base of the Coal Cliff Sandstone which he correlates with various marine sequences worldwide where the isotope ratio falls at the Permo-Triassic boundary. The tracks thus lie close to the Permo-Triassic boundary; evidence for them being latest Permian or earliest Triassic is equivocal.

Conclusions

Evidence of tetrapod occupation of the Sydney Basin in the Late Permian is widespread with body fossils to the north and west and trackways to the south-east. Both amphibians and early amniotes are represented but apart from the temnospondyl from Airly none of the material is further identifiable. The new material from the West Wallsend Colliery constitutes the second oldest vertebrate record from the Permian of Australia.

ACKNOWLEDGMENTS. I am grateful to Bruce Ross for finding the material at West Wallsend, drawing the attention of the Australian Museum to it, and donating all the West Wallsend material to the Museum, and Rod Austin, managing director of Oceanic Coal Australia Ltd, for supporting him. Mr A. Wright found the trackway from the Oakdale Colliery. Clinton Foster of the Australian Geological Survey Organisation was invaluable with stratigraphic advice. Alex Ritchie of the Australian Museum showed me the West Wallsend specimens, while Bob Jones allowed me to borrow them and other specimens from the Australian Museum. John Pickett (Geological Survey of New South Wales) was generous with time and information about the Airly specimen and the Bellambi track, while Ian Percival of the same organisation lent specimens. Per Ahlberg advised me on the distribution of folded teeth in fish. Russell Baader of the La Trobe University Photographic Unit took the photographs. The research was funded by a La Trobe University Special Grant.

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Systematics, Ecology and Phylogeny of the Anamixidae (Crustacea: Amphipoda)

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ABSTRACT. Thirteen new species and one new genus are described in the commensal amphipod family Anamixidae, bringing the total to 33 species in three genera. Thirteen species are recorded from the Pacific Ocean, eight from the Indian Ocean and four from the Caribbean. Developmental stages are documented in four species of *Anamixis* Stebbing, 1897 and one species of *Nepanamixis* n.gen. Developmental stages in *Nepanamixis* are profoundly different from those of *Anamixis* and *Paranamixis* Schellenberg, 1938. All new taxa are fully described and figured. Previously described taxa are reviewed and illustrated where necessary.

The cryptic Anamixidae are found in coral reefs and other hard-bottomed, shallow, tropical waters. An unusual tropical relic, *A. tangaroa* n.sp., is described from cold waters in the Bass Strait, Australia. Current species distributions and information probably reflect collecting bias as many areas remain uncollected.

Cladistic analysis of the Anamixidae proved informative in the *Nepanamixis–Anamixis* group where adequate specimens of new and existing species were available for examination. Results were less informative for *Paranamixis*.

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Amphipods of the family Anamixidae are commensals in sponges and ascidians and occur throughout the world's tropical and subtropical marine systems. They exhibit an unusual life history pattern involving two highly dissimilar developmental stages that occur simultaneously in the host (Thomas & Barnard, 1983). These two stages are so different they were previously assigned to separate families. Initial, or, "leucomorph" developmental stages (male and female) of different anamixid species are nearly identical, while the transformed, or "anamorph" stage (always male) is distinct for each species. In a remarkable transformation, leucomorph males pass via a single moult to anamorph males. This transformation is accompanied by a number of extreme morphological changes that explain their placement in separate families prior to this discovery. Leucomorphs outnumber anamorphs in the host approximately 10:1. Nearly all leucomorph females are ovigerous. It is not known which male stage (or both) interacts reproductively with the female. The fate of post-brood females remains unknown.

Background

Most of what we know of amphipod taxonomy, ecology and community structure shows a strong temperate bias. Tropical marine systems offer promising avenues of research, but advances are often highly unpredictable because so little is known. Coral reefs are geographically discrete, widespread biological systems that exist within a narrow range of biological and physical conditions. Coral reefs present a complex mosaic of macro and microhabitats (Hay, 1981) e.g., live coral, coral rubble, turf algae, sessile invertebrates, and reef-derived sediments, that allow ecological comparisons to be made. However, the small size of tropical amphipods (2–4 mm) combined with difficulties in obtaining representative collections from reef sites has hindered taxonomic and systematic progress within the group.

Cryptic and commensal reef species form highly localised populations, further minimising dispersive capabilities. For this reason, the author has chosen to focus research efforts primarily on cryptofaunal and commensal amphipods, with the assumption that their morphologies and distributions more clearly reflect evolutionary events than do epifaunal forms that can be widely dispersed and exhibit high phenotypic plasticity (Schram, 1986; Conlan, 1988).

Adequate representative samples of amphipods can be procured only by *in-situ* collection from specific substrates with the use of SCUBA techniques. To obtain representative samples of smaller benthic crustaceans, specific collecting programs must be undertaken. This habitat-intensive approach to collecting has opened a new era in the systematic study of shallow-water marine amphipods and other small invertebrates and has provided much new and exciting material for study.

Review of the Anamixidae

Prior to this research there were 13 described species of anamixids, in two genera, *Anamixis* and *Paranamixis*. These two genera were distinguished by the presence (*Anamixis*), or absence (*Paranamixis*), of first gnathopods. The majority of what is known of anamixid biology and ecology has been reported by the author and co-workers (Thomas, 1979, 1981; Thomas & Taylor, 1981; Thomas & Barnard, 1983). Prior to the discovery of the unique transformation process in anamixids (Thomas & Barnard, 1983), leucomorph stages of anamixids were assigned to a separate family, the Leucothoidae. Anamorphs are characterised by having extremely reduced and fleshy mouthparts, in having coxa 1 reduced or vestigial, and in having greatly enlarged second gnathopods and coxae 2–4 that act as a lateral shield to enclose the animal during feeding. Leucomorphs also show various modifications and reductions in structure, but possess only slightly reduced, spinose mouthparts and morphologically unique second gnathopods. Investigations by the author have shown that the transformation moult is not terminal and can be followed by several instars. Before discovery of the transformational process leucomorphs had been assigned to a number of species in the genus *Leucothoides* Shoemaker, 1933 in the Leucothoidae. Leucomorph stages of major anamixid groups are, in most instances, nearly identical and cannot be readily separated at the species level with the exception of the more primitive groups where both stages have morphologically distinct first and second gnathopods. In cases where the transformation process has been documented, or both stages collected *in-situ* from their invertebrate hosts, specific identifications can be made. These combinations of circumstances have produced an extremely tangled taxonomy.

Documentation of the transformation process in anamixids created a sizeable taxonomic problem, because there were now a dozen described species of *Leucothoides* with no possibility to associate them with their anamorph counterparts. This can only be accomplished by collecting the stages *in-situ* from their specific hosts, or by confirmation through rearing experiments that document the transformation process (Thomas & Barnard, 1983). To date, the author has documented the transformation process or confirmed host specificity for four species of anamixids. For detailed explanations regarding rearing methodologies and host confirmation procedures, see Thomas & Barnard (1983). Developmental information on all other taxa is lacking. It must be emphasised that occurrence of both stages in the same general collection does not necessarily confirm taxonomic relationships because most reef areas contain several anamixid species. Problems in the family with unassociated morphologies restrict primary taxonomic emphasis within anamixids to anamorphs, but because leucomorphs represent early developmental stages, they can be highly informative in determining generic limits and relationships from an ontogenetic perspective.

Distribution

The genus *Paranamixis* appears confined to the Pacific and Indian Ocean basins, while *Anamixis* is widespread, with representatives in all tropical oceans. Members of the more plesiomorphic *Nepanamixis* n.gen., are distributed as possible Gondwanaland relicts across the Indian and Pacific Oceans and the Caribbean Sea (Newman, 1991).

Ecology

Host associations for anamixids (when known) are the interior of small asconoid sponges and the branchial cavity of solitary and compound tunicates where the amphipods utilise host-generated currents to filter fine particulates. Where associations are known, anamixids appear highly specific in the choice of host and are either restricted to a particular host species, or in the case of multiple host species, are restricted to similar-sized interior feeding chambers. Unfortunately, host and ecological data are only available for a handful of species (Thomas & Barnard, 1983).

Information from host data, feeding behaviour, and distribution patterns can be valuable sources of information in phylogenetic studies. Observations from

natural history studies and in-situ observations can aid in interpreting convergent morphologies in certain structures. An example of this approach are attempts by the author to evaluate the presence of similar lateral ridges on the cephalic margin of anamixid species in different genera such as *A. vanga* and *P. kanu*. Ecological studies have shown these ridges are present only in those species inhabiting large solitary ascidian hosts, thus, this character probably reflects convergent adaptations to similar feeding strategies and not similar evolutionary histories. Such ecological information can assist in hypotheses addressing the evolutionary significance of a given morphology. In this regard the author agrees strongly with Brusca (1984) who stated similar views regarding isopods.

Selected taxonomic characters

The following characters are some of the more important for taxonomic purposes in the Anamixidae:

Head region: The presence or absence of a lateral keel on the head that serves to align the head against coxa 2 when the head is flexed ventrally during feeding. The morphology and microstructure of the ventral keel located in the mid-region on the ventral portion of the head. The relative length of antennae 1 and 2, and enlargement of the first peduncular segment of antenna 1.

Mouthparts: Standard light microscopy provides limited information on the microstructure of the mouthpart field, except in the case of the elongate and hyper-developed maxilliped palp and prominent ventral keel. Except for the maxilliped palp and ventral keel, the remaining mouthparts are reduced, fleshy and transparent in anamorph stages and are best observed by SEM or differential interference contrast microscopy. The maxilliped, enlarged and modified for food-handling, exhibits various reductions and degrees of fusion in the inner plates, while the outer plates bear vestigial inner lobes in the more plesiomorphic taxa.

Coxal morphology: The general size and dominance of various coxae, their shape and ornamentation can be important features. The morphology and amount of reduction in coxa 1 are important at the generic level. The morphology and ornamentation of the margins of the relatively larger coxae 2–4 are important at the species level, as is the relative dominance of coxae 2–4.

Gnathopods: Gnathopod 1 is present and reduced in most species of *Anamixis*, except for *A. jebbi* n.sp., where it is vestigial in transformed males. In *Paranamixis*, gnathopod 1 is lacking in all post-transformational anamorphs. However, the author has documented tiny vestiges of gnathopod 1 in 2 species of *Paranamixis*, assumed to persist at the transformational moult itself, a remnant of the leucomorph stage. All subsequent stages of *Paranamixis* are characterised by the complete lack of gnathopod 1 in post-transformational anamorphs. When gnathopod 1 is present, the general morphology and dimensions of article 5 (carpus) are important at the generic and specific levels. Patterns of armament and terminal ornamentation of article 6 are informative at the specific level. Anamorphs of *Nepanamixis* n.gen., possess a distinct gnathopod 1 with a basally-expanded carpus, and a linear gnathopod 2 with a geniculate carpal lobe, differing from all other species and underscoring the taxonomic importance of these appendages. Leucomorphs of *Nepanamixis* n.gen., also exhibit a unique configuration of gnathopods 1 and 2, further distinguishing them from all other juvenile anamixid morphs, providing a means of identifying the presence of *Nepanamixis* n.gen., in collections, even when anamorphs are lacking. Gnathopod 2 is greatly enlarged and modified for filter feeding and possesses a number of morphological and morphometric characters of value such as accessory ornamentation (spines, cusps, ridges, long setae) of article 2 (basis); the presence or absence of a serrate carpal ridge (either lateral or medial) on article 5 (carpus); the shape, armament, and morphometrics of article 6 (propodus); the shape, morphology and armament of the dactyl (article 7). The large second gnathopods bear mediofacial setae on the propodus that are used in filter feeding. *Nepanamixis* has two rows of this specialised seta, while *Anamixis* and *Paranamixis* both have a single row. Leucomorph stages possess unique second gnathopods that differ substantially from anamorph forms, being relatively smaller in size and having a prominent transverse palm.

Uropods: Anamorphs differ from leucomorphs in having the outer rami of uropods 2 and 3 reduced to about half the length of the inner ramus. Two species of *Paranamixis* have uropods and peduncles completely lacking spines. All other taxa have spines on the rami and peduncles of uropods 1–3.

Some characters may be especially difficult to observe under normal light microscopy and previous descriptions may be deficient in many cases in enumerating these features. For example, the lateral serrate ridge on the basis of gnathopod 2 in *P. clarkae* is hard to distinguish without Nomarski or phase contrast microscopy. The condition of the apices of the inner plates of the maxilliped is another situation that requires careful examination to accurately assess. Caution must be used in the analysis and interpretation of minute or hard to observe structures. This is especially true in constructing character transformation series for cladistic analysis. There is no substitute for careful and thorough examination of material, however, there are times when specimens are not available for examination and existing descriptions and illustrations lack the minute detail now required in taxonomic descriptions. In these circumstances, the taxonomist must make the best use of available character data.

Methodology

1. Thirteen new species and one new genus are described based on detailed character analysis.

2. Available type material are reviewed in cases where original species descriptions and figures were not adequate to interpret important taxonomic characters.

3. When type material was not available, comparative materials of extant species were used in efforts to resolve taxonomic problems. Material of several species, notably *A. stebbingi, P. bocki* and *P. madagascarensis*, was unavailable for analysis and use of character information was limited to the original descriptions of these species.

4. A detailed study of morphological characters was undertaken to more clearly define selected characters of primary taxonomic importance that would help in the development and interpretation of character state transformation series.

5. Ecological studies of host preference relationships were carried out in an effort to determine whether particular types of associations demonstrated any relationship(s) to selected morphological characters exhibited by the amphipods.

6. Attempts to associate leucomorphs with anamorph counterparts by rearing and/or host confirmation studies have confirmed four leucomorph stages.

7. A complete monographic treatment of the Anamixidae (primarily anamorphs) is presented, with revised family, generic, and specific diagnoses, with keys to all groups. This treatment includes an estimation of anamixid phylogeny generated by the computer program HENNIG86.

Holotypes of all new species have been deposited in the U.S. National Museum (USNM) and the Australian Museum (AM), except where prior arrangements were made with other institutions. Excess specimens will be distributed to interested museum departments that currently house substantial amphipod collections.

Computerised numerical phylogenetic programs were used to produce several trees that were most parsimonious and well resolved. There were no existing cladistic hypotheses to test, either of marine amphipods in general, or tropical amphipods in particular. Distribution patterns represented in the tree(s) (e.g., taxon-area cladograms) were used to infer ancestor-descendant relationships and distribution patterns.

Figure abbreviations (used in specimen drawings). Capital letters in figures refer to parts; lower case letters to the left of capital letters refer to specimens cited in legends and voucher material in the text; lower case letters to the right of capital letters refer to adjectives described below. A—antenna, B—body, C—head, D—dactyl of gnathopod or pereopod, E—coxa, F—accessory flagellum, G—gnathopod, H—peduncle, I—inner plate/ramus, K—ventral keel, M—mandible, O—outer plate/ramus, P—pereopod, R—uropod, T—telson, U—urosome, V—palp, W—pleon, X—maxilliped.

Lower case letters on the left side of labels denote specimens cited in the legends and voucher material in the text; lower case letters on the right side of the labels (or affixed to the drawings as is often the case) indicate the following: c—carpus, d—dorsal, e—broken, f—flat, h—half, i—medial, l—lateral, ll—lower lip, m—medial, n—oblique, o—opposite, p—distal, r—proximal, s—setae removed, t—right, u—left, v—ventral y—enlarged.

Letters in quotation marks are redrawn from previous figures, the drawing using the first letter of the species name.

Taxonomy

Anamixidae Stebbing, 1897

Diagnosis. Accessory flagellum minute, 1–2 articulate, or lacking. Pereonite 1 with lateral locking ridge. Mouthparts reduced in size and complexity, especially in terminal males. Mandible lacking molar. Inner plates of maxilliped reduced, partially to completely fused; outer plates with inner lobes reduced or absent. Coxa 1 much smaller than coxa 2. Coxae 2–4 enlarged; coxa 2 usually subequal to or dominant to coxae 3–4, coxa 3 occasionally dominant. Margins of coxae 2–4 smooth, anterior margin variously expanded, produced, or cuspate, usually with subapical setae. Gnathopod 1 reduced, vestigial, or absent; carpochelate. Gnathopod 2 greatly enlarged, carpochelate.

Description. Based on transformed males: Body laterally compressed, smooth, slick and shiny. Rostrum small to large and thick; lateral cephalic lobes weak, eyes ommatidial. Antenna 1 slender, often partially attached to rostrum, peduncle long, article 2 often as long as 1, main flagellum sparsely articulate, accessory flagellum vestigial or absent, rarely 2-articulate. Antenna 2 slender, feeble.

Mouthparts in terminal males (anamorphs) as follows: Epistome strongly produced anteriorly, front of head with midventral keel; labrum asymmetrically incised. Mouthparts except maxilliped extremely reduced, fleshy and vestigial, dominated by midventral keel. Mandibular palp vestigial, represented by setae; upper and lower lips, maxillae 1 and 2, lacking any spination or ornamentation. Maxilliped enlarged, inner plates reduced, partially or completely fused; outer plates reduced with inner lobes present or absent, when present represented by small medial process; palp 4-articulate, articles 1 and 2 with medial setae; articles 3 and 4 with multiple rows of parallel setae giving rugose appearance, palp article 4 elongate.

Mouthparts in females and non-transformed males (leucomorphs) as follows: Mandibles lacking molar, raker row long, incisors broad, toothed, wavy or with only one lateral notch, palp slender, feeble, 1- or 3-articulate, article 3 short, setae sparse. Labium with inner lobes discrete or fused to outer, gape moderate to absent, mandibular lobes well developed. Inner plates of maxilla 1 small, naked or sparsely setose, outer plate with 5–9 spines, palp 1- or 2-articulate. Maxilla 2 feeble, inner plate broad, medial setae sparse but thick and short, spine-like outer plate much more slender and sparsely setose. Outer plates of maxillipeds moderately developed to absent, inner plates small, small and discrete or mostly fused together or vestigial, palp of maxilliped long, thin, 4-articulate.

Coxa 1 hidden by shield-like coxae 2–4; coxa 2 (or 3) largest, 4 scarcely larger or smaller than 3, weakly excavate or not, ventral margin produced or not; coxae 5–6 smaller, bilobed, hind margin of 6 deeper than 5; coxa 7 entire. Gnathopod 1 small, vestigial, or absent, carpochelate, often 6-articulate. Gnathopod 2 very large and often strongly carpochelate; carpus furnished with dense tufts of medial feeding setae; hand large in males and some females, elongate, oval, weakly to strongly sculptured, palm transverse, oblique, or absent, with 1 or 2 dense rows of mediofacial setae; dactyl long, overlapping hand and carpal process.

Pereopods 3–4 slender, reaching same extent. Pereopods 5–7 alike, short, bases expanded, 7 often lobate or serrate. Pleopods biramous, multiarticulate.

Uropods 1–3 slender, reaching same extent or outer ramus shortened, uropod 3 often breaking; rami lanceolate, outer ramus on 1–2 strongly shortened, on 3 moderately shortened, ramal spines absent to moderate. Telson short to long, ovate, entire.

Gills present on gnathopod 2 to pereopod 6, small, simple, ovate.

Sexual dimorphism. Largely seen in transformed males. Mouthparts except maxillipeds becoming reduced or vestigial, dominated by ventral keel; inner plates of maxilliped becoming severely reduced and partially or completely fused; inner lobes of outer plates becoming reduced or absent. Female gnathopod 2 relatively smaller than non-transformed males, with moderate carpal lobe, distinct palm, and recurved dactyl fitting palm. Oostegites present on pereopods 3–5, typical, with marginal setae. Transformed males with reduced coxa 1 and enlarged gnathopod 2, with carpal process and dactyl immense.

Remarks. The Anamixidae and some Leucothoidae have been assumed in the past to be piercing and sucking inquilines, usually found in warm shallow waters on sessile invertebrates, particularly sponges, tunicates, coral, and perhaps hydroids. However, Thomas & Taylor (1981) found *A. cavatura* to be filter feeders, inhabiting the interior cavities of the hosts where they utilise host-generated currents to filter out food particles on the carpal lobes of the enlarged second gnathopods. The presence of the "piercing stylet" (ventral keel) is not used to pierce host tissue in a parasitic feeding mode, but is instead used to align the large antennal peduncles when they are folded down for feeding, allowing the antennal flagella to be freely articulate during feeding. Thomas & Barnard (1983) also found leucomorphs to be filter feeders, occupying the host in larger numbers with their anamorph counterparts.

Taxonomy. The discovery of the remarkable transformation process by Thomas & Barnard (1983) created sizeable taxonomic confusion because females and non-transformed males had been placed in the genus *Leucothoides* in the Leucothoidae. By redefining the Anamixidae to include only leucothoid-like taxa with reduced coxa 1, *Leucothoides* became a synonym of *Anamixis*. This left a number of anamixids known only from brief descriptions, only one of which allowed specific assignment to an anamorph counterpart (*L. pottsi* = *A. cavatura*). While the transformed males are distinctive, females and non-transformed females of different species exhibit only minute differences and can only be placed to species with certainty by rearing or host confirmation studies. It cannot be assumed that unassigned leucomorphs belong to the common anamorph in an area because extensive collecting efforts by the author have shown that most localities yield multiple species of anamixids, each with their own specific leucomorph.

Investigations by the author show leucomorphs of *Anamixis* and *Paranamixis* to be similar, whereas leucomorphs of *Nepanamixis* are quite distinct. Because of the lack of complete information regarding leucomorphs, taxonomy of anamixids is, of necessity, based primarily on anamorphs. However, because leucomorphs represent developmental stages, consistent morphological differences exhibited at this stage can provide valuable information on evolutionary relationships. For instance, the morphological differences between leucomorphs of *Nepanamixis* and those of *Anamixis* and *Paranamixis* provide strong evidence for *Nepanamixis* as a plesiomorphic genus, ancestral to both *Paranamixis* and *Anamixis*.

Keys to Genera of Anamixidae

(Terminal Males)

KEY I

1. Gnathopod 1 present, article 5 basally inflated ..... *Nepanamixis* n.gen.

—— Gnathopod 1 present, absent, or vestigial. If present, article 5 basally thin 2

2. Gnathopod 1 present, occasionally vestigial ..... *Anamixis*

—— Gnathopod 1 absent ..... *Paranamixis*

KEY II

1. Eyes with 9 ommatidia; maxilliped with inner plates cleft more than one-half, outer plates with inner lobes; carpus of gnathopod 1 basally expanded; coxa 1 moderately reduced, approximately one-half the width of coxa 2; gnathopod 2 with serrate ridge on carpal lobe, propodus with 2 rows of mediofacial feeding setae; ventral margin of coxa 4 crenulate or emarginate; telson triangular ..... *Nepanamixis* n.gen.

—— Eyes normally with 12–20+ ommatidia, occasionally 7; maxilliped, inner plates fused or with apical notch or cleft, outer plates lacking inner lobes; coxa 1 greatly reduced, approximately one-quarter or less the width of coxa 2; gnathopod 2 with carpal lobe smooth or serrate, propodus with 1 row of mediofacial feeding setae; ventral margin of coxa 4 rounded; telson ovate 2

2. Gnathopod 1 present (vestigial in *Anamixis jebbi*) ..... *Anamixis*

—— Gnathopod 1 absent ..... *Paranamixis*

Anamixis Stebbing

Anamixis Stebbing, 1897: 35.
Leucothoides Shoemaker, 1933: 249.

Type species. *Anamixis hanseni* Stebbing, 1897 by monotypy; *Leucothoides pottsi* Shoemaker, 1933, by monotypy.

Diagnosis. In terminal males: Antennae long; anterior margin of head oblique or transverse, with or without anteroventral cusp; eyes with ommatidia compact and numerous, or reduced in number and diffuse; inner plates of maxilliped fused into apically rounded process, or with apical notch, outer plates lacking inner lobes in most taxa. Coxa 1 greatly reduced, remainder of gnathopod 1 present, small, occasionally reduced to fleshy remnant; carpus not inflated basally. Gnathopod 2, propodus with single row of mediofacial feeding setae. Telson 1.1–1.6 longer than wide.

Variables. Head, differing in morphology on lateral, anterior and ventral margins; morphology of ventral keel; in shape and morphology of coxae 2–4; in shape and ornamentation of gnathopods 1 and 2.

Relationships. Differing from *Paranamixis* in the apically fused inner plates of the maxilliped and in presence of gnathopod 1 in post-transformational anamorphs. Differing from *Nepanamixis* in the relatively longer antennae, more numerous ommatidia, smaller coxa 1, in the carpus of gnathopod 1 thinner and lacking prominent cusps; in having gnathopod 2 with single row of mediofacial feeding setae, and the shorter telson.

Leucomorphs of *Anamixis* and *Paranamixis* are distinguished at the specific level by minute characters. *Anamixis* leucomorphs differ from *Nepanamixis* leucomorphs in having fewer ommatidia, a longer carpal lobe with only 2 embedded spines in gnathopod 1, and a more transverse palm in gnathopod 2. However, due to the present inadequate knowledge regarding leucomorphs of all three anamixid genera, characters of the few known leucomorphs cannot be construed as all-inclusive. While some leucomorph characters are highly informative, taxonomy of anamixids must be weighted toward morphological characters exhibited in all taxa. Thus, gnathopod 1, while of possible contradictory value, is retained as an important descriptive character until more complete character information becomes available.

Species: *Anamixis aldabra* n.sp.; *A. barnardi* Sasidharan, 1983; *A. bazimut* n.sp.; *A. cavatura* n.sp.; *A. excalibur* n.sp.; *A. falarikia* J.L. Barnard, 1965; *A. hanseni* Stebbing, 1897 (not Thomas 1979, 1981, 1983); *A. jebbi* n.sp.; *A. kateluensis* n.sp.; *A. mahe* n.sp.; *A. moana* here designated, J.L. Barnard, 1970 (*A. stebbingi*); *A. nedcampensis* n.sp.; *A. ningaloo* n.sp.; *A. pacifica* J.L. Barnard, 1955, 1969, 1979 (= *A. linsleyi*); *A. papuaensis* n.sp.; *A. stebbingi* Walker, 1904 (?Nayar, 1967) not Barnard, 1965, 1970, 1971; *A. tangaroa* n.sp.; *A. torrida* J.L. Barnard, 1974, (anamorph unknown); *A. vanga* n.sp.; *A. yarrega* (J.L. Barnard, 1974).

Other records. Recorded as leucomorphs: species V (Loggerhead Key) J.L. Barnard, 1974; species Q (Albatross) J.L. Barnard, 1974; species 2 from Micronesia, J.L. Barnard, 1974; species, J.L. Barnard, 1974; species (*A. pottsi* of Hirayama, 1983).

Distribution. Marine, Indo-Pacific, Micronesia, Caribbean, Western Atlantic, primarily warm shallows, especially coral reefs, endocommensals with sponges and ascidians, 0–89 m, 19 species as anamorphs, otherwise 18 species.

Key to the Species of *Anamixis*

(*Anamixis stebbingi* excluded because character data unavailable)

1. Article 2 of gnathopod 2 with 3 or more long setae on anterior margin 2

—— Article 2 of gnathopod 2 lacking long setae on anterior margin 3

2. Gnathopod 1 geniculate, reduced in size, but of normal proportions for genus, articles distinct; gnathopod 2, coxa produced into a sharp process midapically, article 2 with 10 or more numerous long setae on anterior margin ..... *A. aldabra* n.sp.

—— Gnathopod 1 greatly reduced, barely visible as a shrivelled appendage, articles indistinct; gnathopod 2, coxa rounded midapically, article 2 with 3 long setae on anterior margin ..... *A. jebbi* n.sp.

3. Carpal lobe of gnathopod 2 with thumb-like process 4

—— Carpal lobe of gnathopod 2 lacking thumb-like process 6

4. Gnathopod 1, articles 5 and 6 with 2 and 1 long apical setae respectively ..... *A. mahe* n.sp.

—— Gnathopod 1, articles 5 and 6 lacking long apical setae 5

5. Coxa 4, ventral margin convex; gnathopod 1, article 5 longer than article 6, apex dilated; gnathopod 2, mesoproximal border of carpus smooth ..... *A. nedcampensis* n.sp.

—— Coxa 4, ventral margin concave; gnathopod 1, article 5 subequal to article 6 in length, apex tapered; gnathopod 2, mesoproximal border of carpus denticulate ..... *A. barnardi*

6. Gnathopod 1, articles 5 and 6 each with long terminal seta, or article 6 with terminal spine 7

—— Gnathopod 1, articles 5 and 6 lacking terminal ornamentation 10

7. Gnathopod 1, articles 5 and 6 each with long terminal seta, 0.5 times the length of each article 8

—— Gnathopod 1, article 5 lacking ornamentation, article 6 with terminal spine, 0.3 times the length of article ..... *A. pacifica*

8. Lateral margins of head rounded, ventral keel sharp 9

—— Lateral margins of head excavate; ventral keel truncate ..... *A. vanga* n.sp.

9. Anterior margin of head oblique, lacking any defining process; anterior margin of ventral keel with small teeth; article 6 of gnathopod 2 elongate, 3.0–3.1 times longer than wide, inner margin of dactyl smooth ..... *A. hanseni*

—— Anterior margin of head transverse, defined by cusp at anteroventral corner; anterior margin of ventral keel smooth; article 6 of gnathopod 2 not elongate, 2.1–2.2 times longer than wide; inner margin of dactyl tuberculate ..... *A. cavatura* n.sp.

10. Head enlarged, anteroventral corner defined by large process; first peduncular segment of antenna 1 enlarged; palp article 4 of maxilliped elongate, 1.9 times length of article 3 11

—— Head not enlarged, anteroventral corner defined by small cusp or process; palp article 4 of maxilliped, 1.1 –1.8 times the length of article 3 13

11. Ventral keel a wide triangular process; gnathopod 2, coxa immense, greatly exceeding coxa 3–4 in size, carpal lobe less than one-half of propodus, hindmargin of propodus oblique with numerous serrations or teeth 12

—— Ventral keel sabre-shaped, extending well below ventral margin of head; gnathopod 2, coxa narrow, smaller than 3 or 4, carpal lobe reaching end of propodus, hindmargin of propodus rectilinear with 3 major teeth ..... *A. excalibur* n.sp.

12. Gnathopod 2: carpal lobe serrate; propodus with large cuspate basomedial process; hindmargin of propodus with small serrations; dactyl with 2 processes on inner margin, apex excavate ..... *A. papuaensis* n.sp.

—— Gnathopod 2: carpal lobe smooth; propodus lacking basomedial process; hindmargin of propodus with 5 major teeth; inner margin of dactyl smooth, apex bifid ..... *A. falarikia*

13. Gnathopod 2: carpal lobe straight, blunt, reaching to end of propodus; propodus rectilinear, hindmargin straight, unarmed; inner margin of dactyl unarmed. Inner plates of maxilliped apically notched or broadly truncate 14

—— Gnathopod 2: carpal lobe either long and recurved, or if short, blunt; propodus not rectilinear, hindmargin with oblique palm, with teeth or excavations; inner margin of dactyl armed. Inner plates of maxilliped apically rounded or cleft 16

14. Antenna 2 shorter than 1; coxa 3, ventral margin tapering posteriorly, anterior margin expanded; ventral keel small, anterior margin oblique, posterior margin defined by ventral tooth ..... *A. kateluensis* n.sp.

—— Antenna 2 subequal to 1; coxa 3, ventral margin quadrate, anterior margin straight; ventral keel a broad process, lower margin projecting well below ventral margin of head 15

15. Entire anterior margin of ventral keel perpendicular and parallel to anterior margin of head, distal margin with small anterior-directed tooth; ventral margin of coxa 2 with distinct angular projection ..... *A. bazimut* n.sp.

—— Anterior margin of ventral keel tapering posteriorly into a ventrally projected triangular tooth; ventral margin of coxa 2 with slight midventral angle ..... *A. moana* n.sp.

16. Inner plates of maxilliped apically rounded; coxa 2 ventrally produced; telson 1.3–1.4 times longer than wide 17

—— Inner plates of maxilliped cleft one-third; coxa 2 ventrally excavate; telson 1.7 times longer than wide ..... *A. tangaroa* n.sp.

17. Ventral keel large, sharp, with 3 small anterodistal teeth; gnathopod 2, carpal lobe short and blunt, hindmargin of propodus tapering with 2 major and 2 minor teeth, inner margin of dactyl with 2 processes, the innermost serrate, the outermost with paired setae ..... *A. ningaloo* n.sp.

—— Ventral keel small, truncate, lacking teeth; gnathopod 2, carpal lobe long, recurved, hindmargin of propodus convex, with 1–2 minor cusps, inner margin of dactyl evenly tuberculate ..... *A. yarrega*

Anamixis aldabra n.sp.

Fig. 1

Type material, HOLOTYPE, male "A", 2.52 mm, USNM 235727, forereef slope, Picard Island, Aldabra, Seychelles, formalin wash of coralline algae encrusted coral head, 2.5 m, J.D. Thomas, 17 April 1983, JDT-Ald-19. 1 PARATYPE, male "B", 2.58 mm, USNM 235728, Picard Island, Aldabra, Seychelles, formalin wash of rubble from forereef, 2.5 m, J.D. Thomas, 3 April 1983, JDT-Ald-5a.

Diagnosis. Anterior margin of head transverse. Gnathopod 1, article 6 geniculate. Anteroventral margin of head quadrate. Gnathopod 2, coxa produced into sharp process midventrally; basis with numerous long setae on lower anterior margin; carpus bearing weakly rounded, bifid process near apex. Coxae 3–4 tapering ventrally, anterior margin of coxa 3 expanded.

Description. Head, anteroventral margin quadrate, lacking cusps or other process; antenna 1 ratio 21:15:13; ventral keel scarcely extending below head margin, broadly rounded with slight ventral protuberance; eyes red in 7-year formalin, ommatidia with 16–18 coloured facets, and 2 clear facets at posterior margin of eye. Lower lip lobes not readily visible from lateral view. Antenna 1, article 3 of peduncle much thinner than articles 1–2; flagellum 10-articulate, aesthetascs on articles 8–9. Antenna 2, flagellum 4- or 5-articulate. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.8 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa rounded anteroventrally, bearing 2 small apical setae; propodus exceeding carpus in length, slightly recurved at apex, inner margin serrate with small embedded setae. Gnathopod 2, coxa subequal in size to 3 and 4, lower margin produced into sharp midventral projection, several small setulae embedded submarginally; basis expanded distally, with 12 long setae on anterior and medial surface; carpus inflated and slightly recurved, anterior surface irregular and indented, bearing several small setae, distal portion with an indentation and weakly rounded process near apex bearing a seta, apex furnished with 5 apical and 2 subapical setae; Posterior margin of propodus narrowed posteriorly, row of mediofacial setae extending nearly one half the length of palm, posterior margin with scattered setae, ventral margin defined by quadrate process laterally, medial margin oblique; dactyl straight, unarmed, bearing 2 setae on small rounded process. Pereopod 3, coxa with anterior margin expanded, apex broadly rounded and tapering posteriorly, with 5–6 submarginal setae; posterior margin defined by small cusp; remainder of pereopod normal. Pereopod 4, coxa rounded ventrally, tapering posteriorly, 5–6 submarginal setae present, posterior margin expanded at midpoint, then tapering forward to pereonite; remainder of pereopod similar to pereopod 3. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, evenly rounded posteriorly. Pereopod 7, coxa entire; basis spinose anteriorly, posterior margin with several notches bearing setae. Uropods 1 and 2, outer ramus about one-half the length of inner ramus. Uropod 3 missing. Telson 1.9 times longer than wide, with 2 apical setae and two pairs of dorsofacial setae.

Etymology. Named for the type locality, Aldabra Atoll, a noun in apposition.

Relationship. *Anamixis aldabra* is distinct in bearing numerous long setae on the basis of gnathopod 2, and in having a geniculate propodus on the first gnathopod. *Anamixis aldabra* appears to show no clear affinities to its nearest geographic neighbour, *A. mahe*. While both species have a process on the carpal lobe of gnathopod 2, *A. aldabra* lacks the serrations found along the proximal carpal margins found in other species of Indian Ocean *Anamixis*, *A. mahe, A. stebbingi* and *A. barnardi*. *Anamixis aldabra* also differs from *A. mahe* in the reduced peduncular article 3 of antenna 1; the quadrate lower margin of the head; the geniculate propodus of gnathopod 1; the morphology of coxae 2–4; the straight dactyl of gnathopod 2; a deeper hind lobe on coxa 6; and a relatively narrower telson. The sharp ventral process found in coxa 2 is widespread in both Indian Ocean and South Pacific taxa. The relative taxonomic value of this character is unclear.

Remarks. Leucomorphs of *A. aldabra* are not confirmed. Leucomorphs have been recorded from Aldabra, but until specific hosts are documented, or rearing experiments confirm relationships, assignment of this material to *A. aldabra* is premature. Colour in freshly preserved material: Antenna 1 and pereonites 1–7 with dorsal and lateral blotches of red; red eye colour persisting in formalin and alcoholated specimens.

Habitat. Specific habitat or host unknown, general habitat preference shallow coral rubble.

Distribution. Indian Ocean, presently known only from the type locality, Aldabra Atoll, coral reefs, 2–3 m.

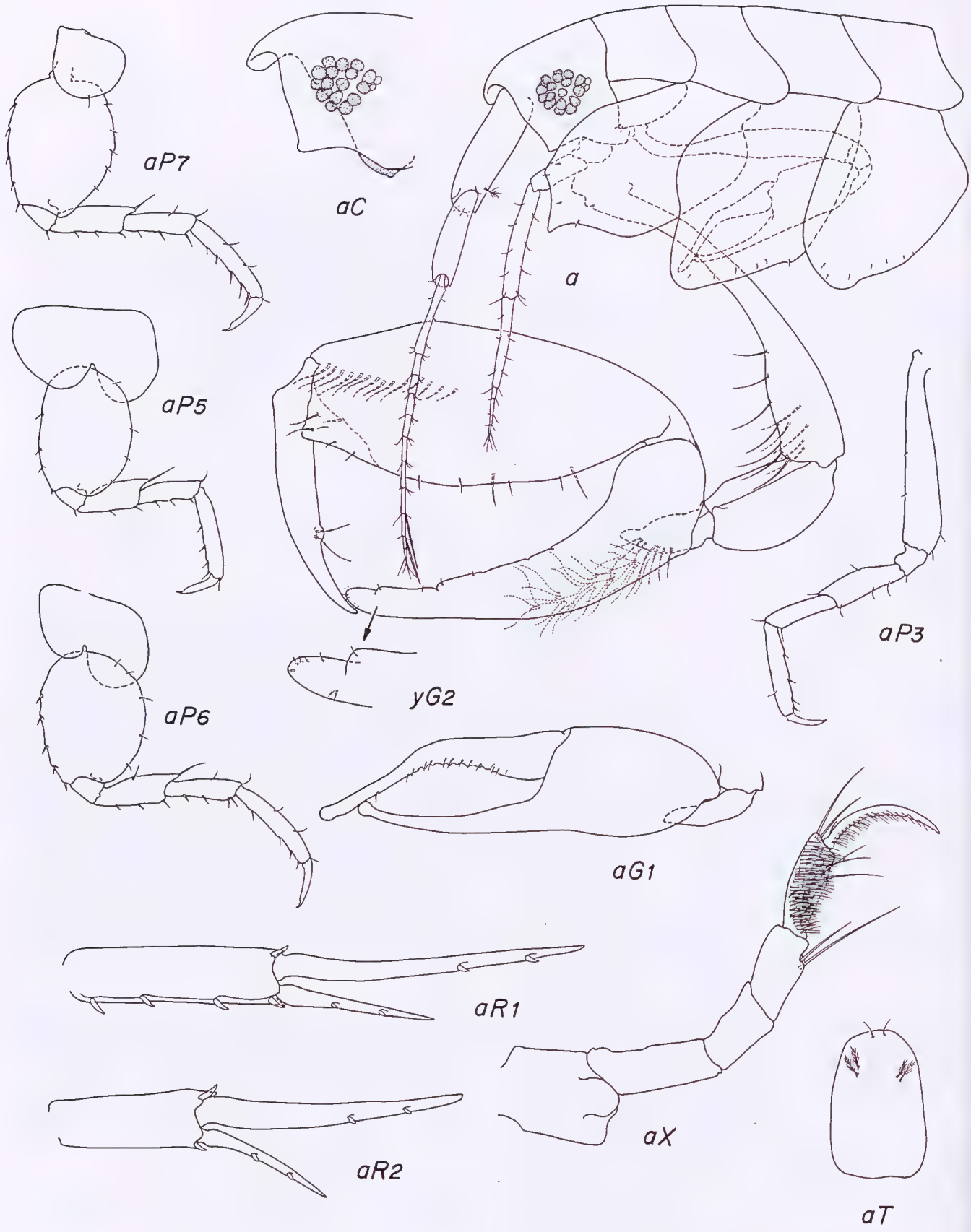

Fig. 1. *Anamixis aldabra* n.sp., holotype, anamorph male "A", 2.52 mm.

Anamixis barnardi Sasidharan, 1983

Anamixis barnardi Sasidharan, 1983: 195–199, figs 1–14.

Diagnosis. Ventral keel rounded; gnathopod 1, articles 5 and 6 with apical setulae; gnathopod 2, carpus bifid laterally, denticulate on proximal margin; coxa 4 emarginate ventrally.

Description. Head, lateral margin rounded, anterior margin transverse, defined ventrally by small cusp, eye composed of compact ommatidia; ventral keel obliquely rounded. Antenna 1, 1.28 the length of head to second pereonite segment, ratio of peduncle segments 1–3, 10:9:6; flagellum subequal to peduncle, 9-articulate. Antenna 2, 1.0 the length of head to second pereonite segment, flagellum short, 4-articulate. Gnathopod 1 lacking terminal setae on articles 5 and 6. Gnathopod 2, coxa subequal to 3–4, rounded, with anterior cusp; lateral margin of carpus with tooth at distal one-third, proximal margin denticulate. Telson, lateral margins slightly expanded, apically rounded, 1.52 times longer than wide.

Relationship. *Anamixis barnardi* forms part of a species complex including *A. mahe* and *A. stebbingi*, all Indian Ocean species that share the following characters: transverse anterior margin of the head defined by a small cusp, a rounded ventral keel; coxae 2–4 subequal in size; carpal lobe of gnathopod denticulate; and coxa 4 ventrally emarginate. *Anamixis mahe, A. barnardi* and *A. nedcampensis* have a prominent carpal tooth on gnathopod 2, however, the proximal denticulations on the carpus occur laterally in *A. mahe*, while they are found on the medial margin in *A. barnardi* and *A. stebbingi*, lacking in *A. nedcampensis*. *Anamixis mahe* also has a much larger and more recurved dactyl than is found in either *A. stebbingi* or *A. barnardi*. Both *A. stebbingi* and *A. barnardi* lack the long terminal setae of articles 5 and 6 of gnathopod 1, a feature apparently unique to *A. mahe*. See *A. stebbingi* for discussion of Nayar's report of *A. stebbingi* from the region.

Habitat. From sponges in littoral waters.

Distribution. Indian Ocean, Krusadi Island, Gulf of Manaar, South India, littoral.

Anamixis bazimut n.sp.

Fig. 2

Type material. HOLOTYPE, anamorph male "A", 2.87 mm, USNM 243318, Tab Anchorage, Madang, Papua New Guinea, gully in south Dam Awan (Rasch Passage), rubble and sediment, 3 m, J.D. Thomas, 22 February 1990, JDT-PNG-57g. PARATYPES, USNM 239493; anamorph male "B", 2.68 mm, Tab Anchorage, Madang, Papua New Guinea, reef flat on south end of Wongad Island, 4–6 m, J. Thomas, 2 May 1991, JDT-PNG 85b; anamorph males "C", 2.80 mm, and "D", 2.31 mm, Madang Harbour, Papua New Guinea, coral rubble and debris in front of Madang Reef Resort, taken from small asconoid sponges, 1 m, 28 February 1990, J. Thomas, A. Myers and J.L. Barnard, JDT-PNG 68a.

Diagnosis. Anterior margin of head transverse, with or without cusp; ventral keel large, projecting well below head, anterior margin transverse, parallel to anterior margin of head, ventral margin defined by anteroventrally directed tooth, anterior margin coxae 2–4 subequal in size, coxa 2, midventral margin produced.

Description. Holotype "A". Head, anterior margin transverse, with small anteroventral cusp; ventral keel broad, anterior margin transverse, extending well below ventral margin of head, anterior margin parallel with anterior margin of head, ventral corner defined by anteroventrally directed tooth; eyes with 18 scattered ommatidia. Antennae: Antenna 1, ratio of peduncle articles 1–3, 28:20:13; flagellum 8-articulate; antenna 2 scarcely shorter than 1; flagellum short, 3- or 4-articulate. Maxilliped, inner plates reduced, tapering, with small apical cleft; outer plates lacking inner lobes; palp article 4, 1.5 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 geniculate, inner margin unarmed; article 6 recurved, inner margin tuberculate with submarginal setae. Gnathopod 2, coxa thinner than 3, more or less subequal to 4, ventral margin produced, angular, bearing 4–5 submarginal setae; carpal lobe long, blunt reaching to end of propodus, apex curved slightly forward; hindmargin of propodus smooth, linear, unadorned, with 5–7 submarginal setae; dactyl with paired setae on inner distomedial margin. Pereopod 3, coxa rectangular, with 4–5 submarginal setae. Pereopod 4, coxa tapering posteriorly, posteroventral margin with slight excavation, bearing 4 submarginal setae. Pereopods 5–6 similar, coxae bilobed, basis spinose anteriorly, posterior margin slightly expanded. Pereopod 7, coxa entire, with 2 submarginal setae in small notches on posteroventral corner. Uropods 1–2, outer rami reduced approximately one-half of inner, spinose. Uropod 3, outer ramus scarcely shorter than inner, spinose. Telson broad, entire, with 2 dorsofacial plumose setae and 2 apical setae.

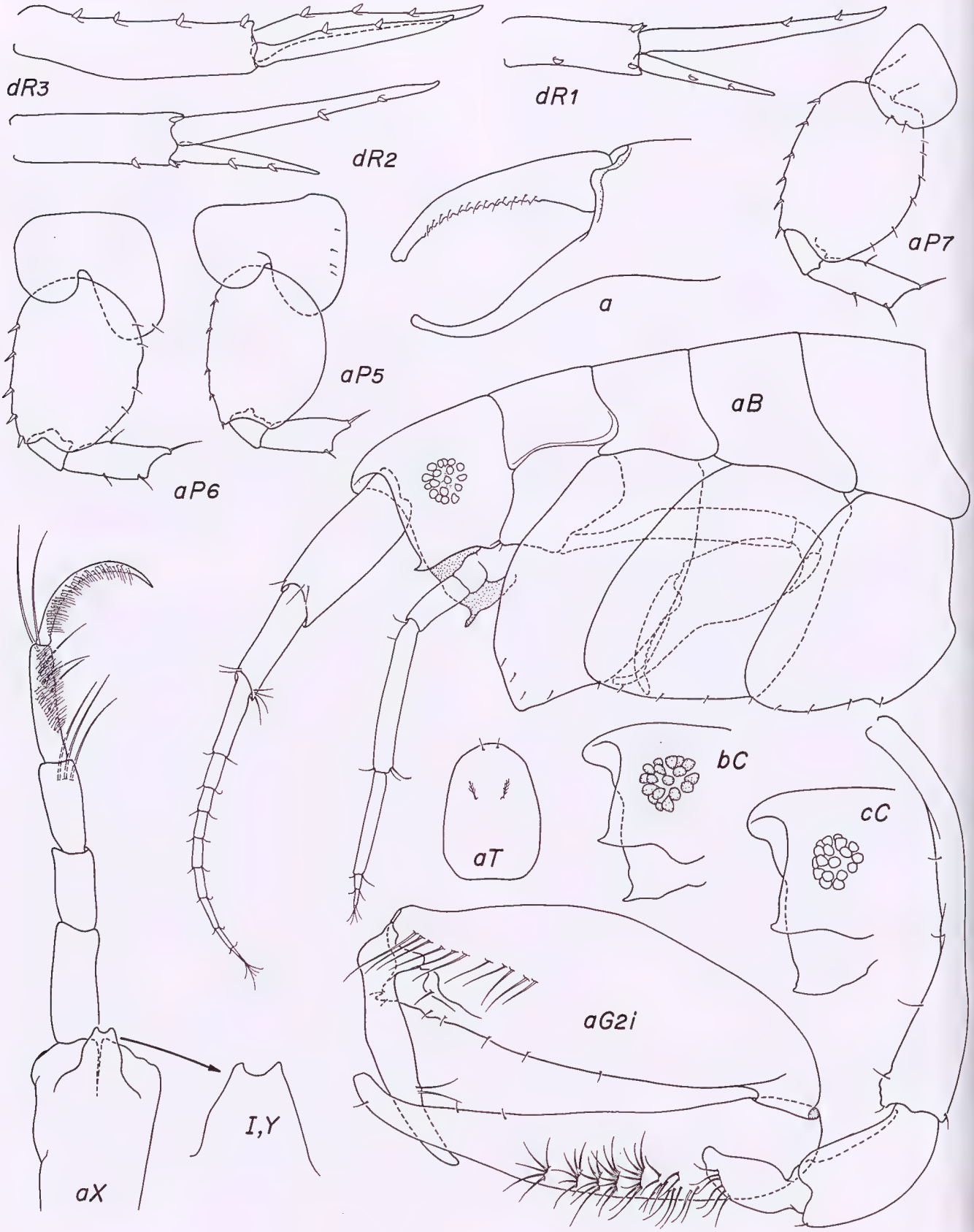

Fig. 2. *Anamixis bazimut* n.sp., holotype anamorph male "A", 2.87 mm; "B", 2.68 mm; "C", 2.80 mm; "D", 2.31 mm.

Leucomorphs. Recorded from small asconoid sponges, undescribed.

Etymology. Pidgin English; named after the Bazimut clan, Riwo District, Madang, who own much of the waters and reefs of Tab Anchorage.

Relationship. *Anamixis bazimut* forms part of a triad of closely related species, including *A. kateluensis* and *A. moana*. These species share the following characters: coxa 2 subequal to 3–4, broad ventral keels extending well below the ventral margin of the head, and general shape and morphology of gnathopod 2. *Anamixis bazimut* and *A. kateluensis* both have apical processes on the inner plate of the maxilliped, whereas *A. moana* exhibits an apically truncate inner plate on the maxilliped. This morphological clade suggests a closer relationship between *A. bazimut* and *A. kateluensis* than either species has to *A. moana*.

Remarks. The *bazimut–kateluensis–moana* clade shows little variation over wide expanses of ocean and may eventually prove to be morphoclines of a previously widespread palaeoendemic of the Pacific Plate. Additional sampling and analysis of specimens are needed to resolve this situation. Application of molecular systematic techniques may also prove informative.

This species has also been collected by the author from Australian coral reefs, Lizard Island south to Orpheus Island, off Townsville.

Habitat. Small asconoid sponges in rubble areas.

Distribution. Bismarck Sea of northern Papua New Guinea to the Coral Sea of northern Queensland, coral reefs, 1–5 m.

Anamixis cavatura n.sp.

Figs 3,4

Anamixis hanseni Thomas, 1979: 107–109; Thomas & Taylor, 1981: 462–467, figs 1–5; Thomas & Barnard, 1983: 154–157 (not *A. hanseni* Stebbing, 1897).

Type material. HOLOTYPE, anamorph male "D", 2.39 mm, USNM 253729, Carrie Bow Cay, Belize, coral rubble from reef flat just behind reef crest near north-east corner of South Water Channel, 1–2 m, J.D. Thomas, 3 July 1987, JDT-Bel-115a; 1 PARATYPE, anamorph male "C", 4.60 mm, USNM 253730, Carrie Bow Cay, Belize, formalin wash of rubble from backreef area of reef bordering South Water Channel, 1 m, J.D. Thomas, 14 July 1987, JDT-Bel-126; 2 PARATYPES, leucomorphs, male "A", 4.41 mm, USNM 253732, and female "B", 3.28 mm, USNM 253733, Carrie Bow Cay, Belize, JDT-Bel-126.

Additional material examined. Anamorph male "K", 4.85 mm, USNM 253731, Coupon Bight, Big Pine Key, Florida Keys, from branchial chamber of the colonial ascidian *Ecteinascidia turbinata* Herdman, 2 m, J.D. Thomas, 1 November 1981.

Diagnosis. Head, rounded laterally, anterior margin oblique, defined by small cusp; ratio of antenna 1 peduncle segments 1–3, 14:12:10; ventral keel prominent, extending beneath head, triangular, slightly recurved anteriorly, ventrally sharp; gnathopod 2, palm with 3–5 distinct cusps, largest near insertion of dactyl, others progressively smaller, dactyl tuberculate. Leucomorph males and females: head angle truncate, nearly 90 degrees, ventral keel produced beneath head, subrectangular; gnathopod 1, coxa tapered, seta present at apex and near notch along posterior margin, carpus, inner margin finely serrate, apex with 2 serrate spines, the larger bifid distally; gnathopod 2, palms transverse.

Description. Transformational anamorph, holotype "D". Head, lateral margins rounded, anterior margin broadly rounded and lacking cusp; eye composed of numerous compact ommatidia. Antenna 1 and 2, 0.37 and 0.28 as long as body. Antenna 1, flagellum with 8-articulate. Antenna 2, flagellum 3-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically produced process; outer plates lacking inner lobes; palp article 4, 1.2 times length of article 3. Pereonite 1 with prominent lateral locking ridge. Gnathopod 1, coxa reduced, distally bifid; carpus, upturned distally, inner margin lacking serrations, apex with long setae; propodus, apex not quite reaching terminus of carpus, inner margin unevenly serrate, apex with long setae. Gnathopod 2, coxa larger than 2 or 3, rounded ventrally, anterior and posterior margins defined by small cusp; basis with small triangular locking process distally; carpus recurved; propodus with 3 teeth; dactyl slightly recurved, with two tubercles on inner margin. Pereopod 3, coxa rounded ventrally, anterior margin with small cusp; remainder of pereopod normal for genus; Pereopod 4, coxa rounded ventrally, posterior margin expanded; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed, hind margin not produced; basis, spinose anteriorly, posterior margin expanded. Pereopod 6, coxa bilobed, hind margin slightly rounded; basis, anterior margin spinose, posterior margin expanded. Pereopod 7, coxa entire; basis spinose anteriorly, posterior margin expanded. Epimera normal. Uropods 1 and 2 with outer ramus reduced. Outer ramus of uropod 3 relatively longer than rami of uropods 1 and 2, not reaching apex of inner ramus. Telson entire, apex produced, 1.46 times longer than wide.

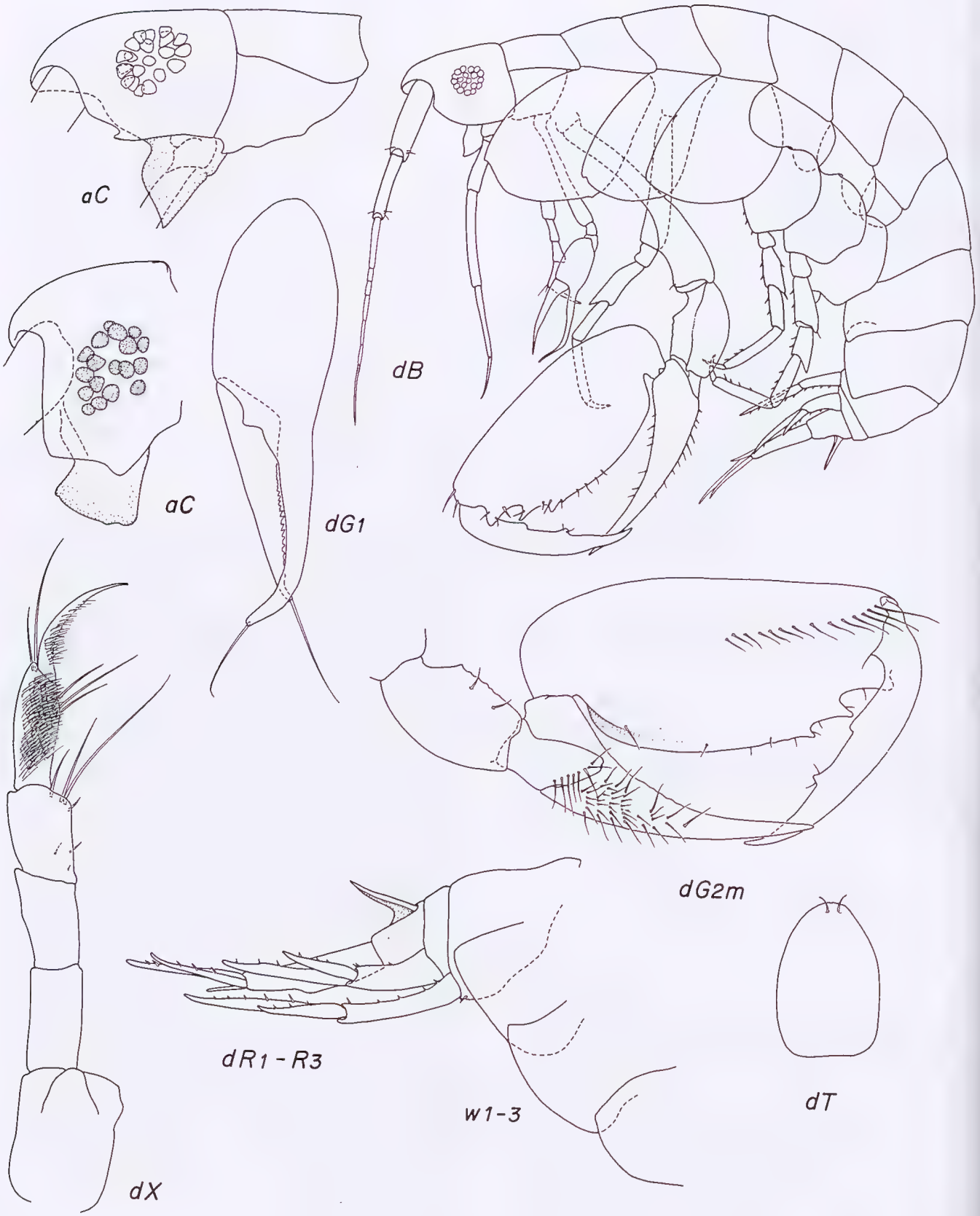

Fig. 3. *Anamixis cavatura* n.sp., holotype, anamorph male "D", 2.39 mm; "A", leucomorph male, 4.41 mm.

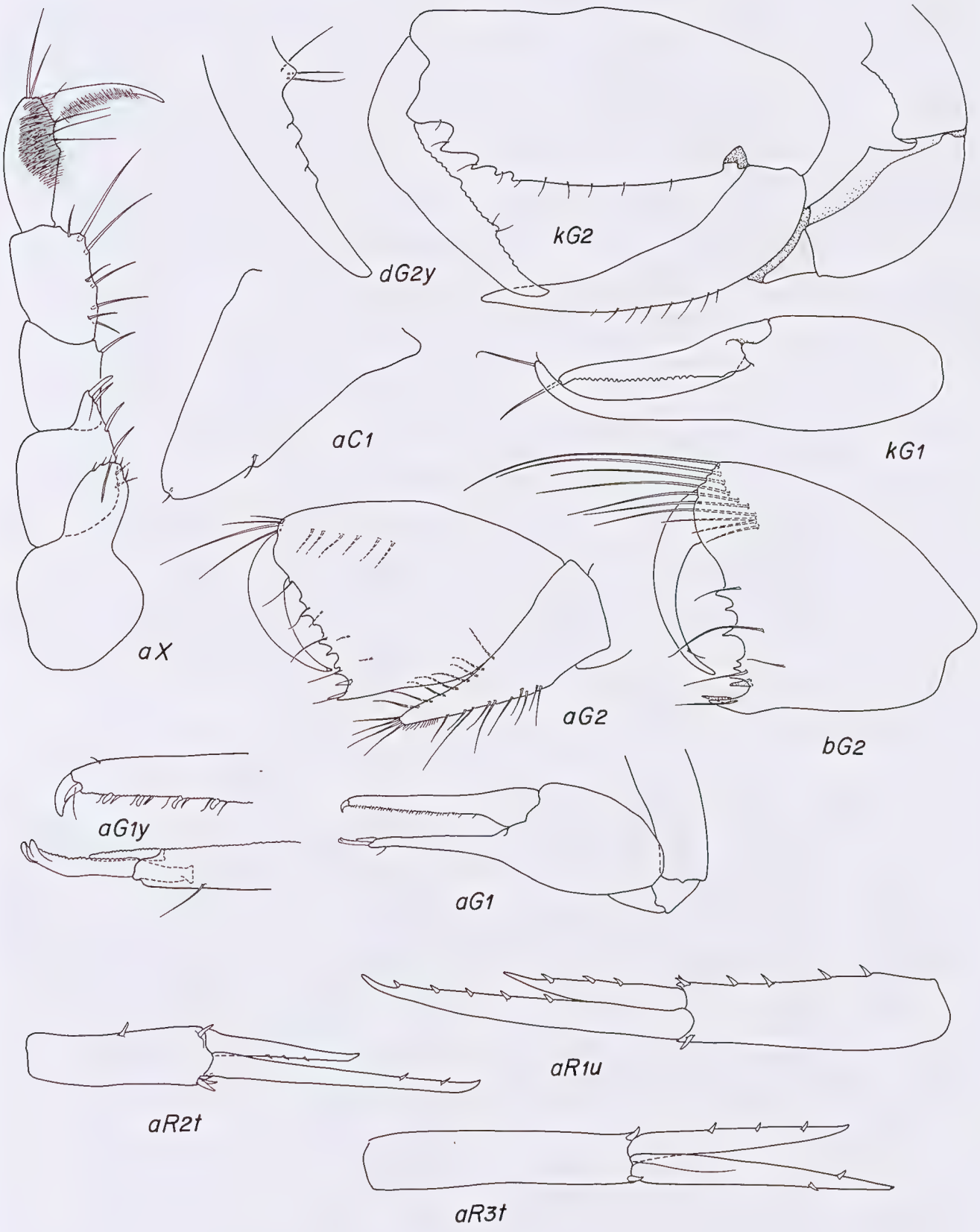

Fig. 4. *Anamixis cavatura* n.sp., holotype, anamorph male "D", 2.39 mm; "A", leucomorph male, 4.41 mm; "B", leucomorph female, 3.28 mm; "K", anamorph male, 4.85 mm.

Leucomorphs. Known from hosts, small asconoid sponges and colonial ascidians. Following description based on male "A", and female "B" from type locality: male, head margin acute, forming sharp angle; ventral keel adze-shaped and slightly extended forward, eye with 18 ommatidia. Mouthparts normal for genus. Gnathopod 1, coxa tapering, with two widely separated small setae, one at apex and one near small posterior cusp; propodus, inner margin finely serrate, apex with 2 embedded spines, inner margins serrate, larger spine bifid distally; propodus, inner margin finely serrate and armed with a series of grouped seta, and small spine surrounding a thicker spine of equal length. Gnathopod 2, palm nearly transverse and bearing approximately 6 short and dispersed feeding setae. Females similar to males except for a relatively smaller second gnathopod, with a more excavate palm, and inner margin of propodus with a dense series of 9 long feeding setae.

Variations. Anamorph specimens from the Florida Keys are consistently larger than specimens from other parts of the Caribbean. This may be due in part to the increased availability of hosts and the relatively greater particulate and nutrient loads that occur in Florida Keys waters compared to other parts of the Caribbean. Morphological variations are documented primarily in the development of a head cusp in post-transformational anamorphs; and in gnathopod 2, where increased size produces the characteristic 5 teeth on the propodus, and tuberculations on the inner margin of the dactyl.

Etymology. From the Latin "cavatura", meaning a hollow or cavern, referring to the interior cavities of hosts.

Remarks. Colour in live material: anamorphs, prominent dorsal and lateral banding of a brilliant reddish-pink colour, coxae 2–4 with a diffuse scattering of this same colour; eyes are a brilliant red. The large second gnathopods have a shiny appearance and are white in colour. Leucomorphs, exoskeleton transparent, gonadal tissue usually visible as brownish dorsal mass; eggs deep green in colour.

Thomas & Taylor (1981) first documented the existence of vestigial mouthparts and the feeding ecology in anamorphs of this species from the host ascidian *Ecteinascidia turbinata*. The normal complement of specimens within the host is 1–2 anamorphs and 5–8 leucomorphs. Methods of reproduction in this and other species are undocumented.

Anamixis cavatura was incorrectly referred to as *A. hanseni* by the author in earlier publications (Thomas, 1979). Considering collected materials and examination of type material, *A. hanseni* appears limited to its type locality, stated as "West Indies" in the original description, but reported to be St. Croix in the Virgin Islands (Dr Jan Stock, Netherlands, personal communication).

Anamixis cavatura differs from *A. hanseni* in the cuspate margin of the head, morphology of the ventral keel, a coxa 2 without marginal cusps, and the shorter propodus of gnathopod 2. Stebbing (1897) shows a series of teeth on the anterior margin of the ventral keel. Unfortunately, the type borrowed from the Copenhagen Museum was missing the head, so that this feature cannot be definitely confirmed. No other specimens from the type locality or its environs are known to exist. *Anamixis cavatura* differs form *A. vanga* in the relatively shorter antennae, cuspate margin of head, lack of a hollowed lateral margin of the head, shape of the ventral keel, in having 5 teeth on the propodus of the second gnathopod (larger specimens), and a shorter row of mediofacial feeding setae. Leucomorphs of the *A. cavatura* are easily distinguished from those of *A. vanga* by the more angular head margin and truncate ventral keel; in gnathopod 1, the tapering coxa with widely separated setae, in having serrations on the apical spines of the carpus, the larger apical spine being bifid, in lacking the larger serrations on the inner margin of the carpus; and in the more transverse palm of gnathopod 2.

Habitat. Internal cavities of small asconoid sponges and colonial ascidians, especially *Ecteinascidia turbinata* Herdman.

Distribution. Western Atlantic Ocean, Ft. Pierce Florida to Biscayne Bay; Gulf of Mexico, Key West to Tampa; Florida Keys, Caribbean Sea, Yucatan, Belize, Honduras, Jamaica, The Bahamas, Greater and Lesser Antilles, 1–5 m.

Anamixis excalibur n.sp.

Fig. 5

Type material. HOLOTYPE, male "A", 2.75 mm, USNM 253734, Banana Reef, Tab Anchorage, Madang, Papua New Guinea, from formalin wash of "penny coral" *Diaseris fragilis*, 30–34 m, J.D. Thomas, 8 February 1990, JDT-PNG-38b; 1 PARATYPE, male "B", USNM 253735, JDT-PNG-38b; 1 PARATYPE, USNM 253744, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of attached rubble, 2–3 m, J. D. Thomas, 27 January 1990, JDT-PNG-24a; 3 PARATYPES, USNM 253737, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble on forereef slope, 12–15 m, J.D. Thomas, 28 January 1990, JDT-PNG-25a; 1 PARATYPE, USNM 253738, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble from 50 m south of marker, bottom mostly rubble and soft corals, 3–4 m, J.D. Thomas, 2 February 1990, JDT-PNG-32a; 1 PARATYPE, USNM 253739, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble from forereef slope, 34 m, J.D. Thomas, 6 February 1990, JDT-PNG-36a; 1 PARATYPE, male "C", USNM 253736, Barracuda Point, East of Tab Island, Madang, Papua New Guinea, formalin wash of rubble from

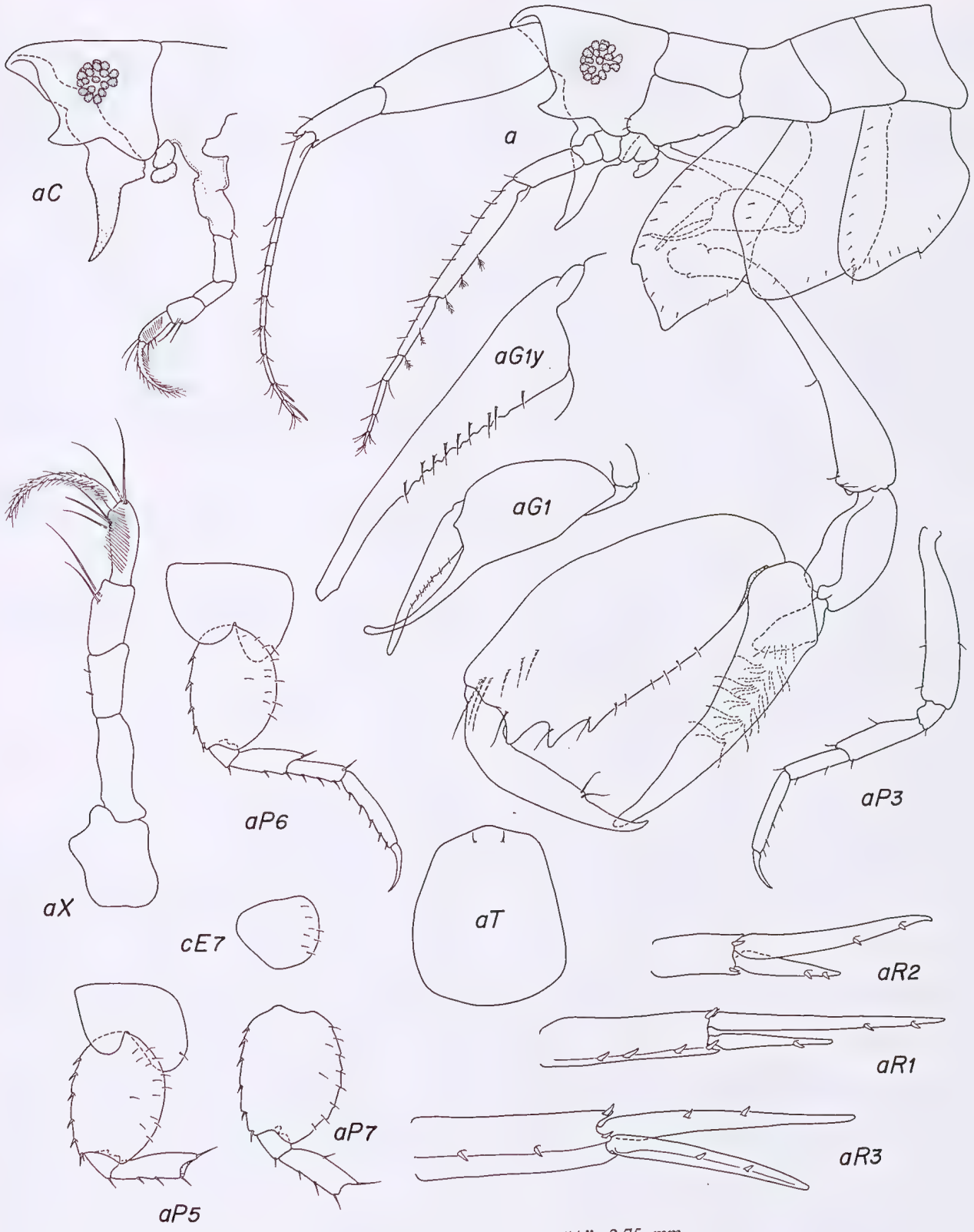

Fig. 5. *Anamixis excalibur* n.sp., holotype, anamorph male "A", 2.75 mm.

forereef slope, 30–33 m, J.D. Thomas, 8 February 1990, JDT-PNG37a; 2 PARATYPES, USNM 253740, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble, 3–4 m, J.D. Thomas, 16 February 1990, JDT-PNG-48a; 1 PARATYPE, USNM 253741, gully in south Dam Awan (Rasch Passage), Tab Anchorage, Madang, Papua New Guinea, formalin wash of dead *Acropora* samples, 4–6 m, J.D. Thomas, 22 February 1990, JDT-PNG-57f; 2 PARATYPES, USNM 253742, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of *Acropora* rubble, 40–55 m, J.D. Thomas, 24 February 1990, JDT-PNG-59a.

Diagnosis. Head enlarged, anteroventral corner defined by a large upturned cusp. Antenna 1, first peduncular segment enlarged, ratio of peduncle segments 1–3, 30:17:16; antenna 2 inserted near posterior margin of eye. Ventral keel prominent, recurved, extending well below margin of head; terminal article of maxilliped palp elongate. Coxa 2 narrow, linear, distally produced; coxa 3 wider than 2 or 4.

Description. Head, anterior margin transverse, anteroventral margin defined by large cuspate process, ventral margin excavate; eye with 20 ommatidia; ventral keel elongate, slightly recurved anteriorly. Antenna 1, article 1 enlarged, equal to articles 2 and 3 in length, flagellum with 8 articles, aesthetascs present on articles 7–8. Antenna 2, peduncle normal, flagellum with 5 articles. Fleshy lobes of lower lip readily visible from lateral view. Maxilliped, inner plates fused into an apically rounded plate; outer plates lacking; palp article 4, 1.9 times length of palp article 3. Pereonite 1 with prominent lateral locking ridge. Gnathopod 1, coxa reduced, rounded anteriorly bearing 2 small setae; carpus slightly recurved; propodus serrate and setose on inner margin. Gnathopod 2, coxa narrow, 2.28 times deeper than wide, apically produced, anterior margin defined by distinct cusp, margins bearing numerous small embedded setulae; basis, anterior margin bearing 2 short setae; carpal lobe with dense tuft of medial setae; propodus with 3 large distal teeth, ventral and posterior margins with short to medium setae, medial surface with short row of long feeding setae near anteroventral margin; dactyl straight, with small process bearing 2 medium setae. Pereopod 3, coxa broad, anterior margin expanded, ventral margin tapering distally, anterodistal margin slightly excavate, posterior margin defined by small cusp, numerous small setulae embedded along margins, remainder of pereopod normal. Pereopod 4, anterior margin of coxa straight, ventral margin rounded distally, posterior margin defined by small cusp, numerous setulae embedded along margins, remainder of pereopod 4 similar to pereopod 3. Pereopods 5–6, coxae bilobed, bearing a single posterior seta; bases, anterior margins spinose, posterior margins evenly rounded bearing numerous small setae. Pereopod 7, coxa small, entire, with numerous small setae; anterior margin of basis spinose, posterior margin weakly serrate, bearing marginal and submarginal setae. Epimera normal for genus. Outer rami of uropods 1 and 2 shortened, outer ramus of uropod 3 only slightly shortened, all rami with 2 spines each, except for the outer ramus of uropod 1 which bears a single spine. Telson broad, 1.2 times longer than wide, apical margin only slightly produced, 2 apical setae.

Etymology. Named for the sword of King Arthur, the mythical mediaeval ruler of Camelot, referring to the elongated ventral keel.

Relationship. *Anamixis excalibur* is distinct in the size and shape of the head, prominent ventral keel, and elongate coxa 2. *Anamixis excalibur* from Papua New Guinea resembles *A. falarikia* from Micronesia in the elongate maxilliped palp article 4, enlarged first peduncular segment on antenna, 1 and large process defining the anteroventral margin of the head; but differs in the linear coxa 2, and in having a more transverse palm with fewer teeth on gnathopod 2, and a longer carpal lobe.

Remarks. Colour of freshly collected material: pereonites 1–7 with faint orange dorsal band, and with a small, prominent orange dot laterally near insertion of coxae; Gnathopod 2 with distinct orange blotch along distal portion of propodus; dactyl with orange bands at base and tip. Colour fading rapidly in preserved material to translucent white. Leucomorphs of this species are currently unknown.

Habitat. Specific host or habitat unknown. General habitat preference algae-covered coral rubble, becoming more common at depths below 12 m.

Distribution. Bismarck Sea, from coral reefs in the Madang region along the north coast of Papua New Guinea, 3–55 m.

Anamixis falarikia J.L. Barnard, 1965

Fig. 6

Anamixis falarikia J.L. Barnard, 1965: 485–488, fig. 3.

Diagnosis. Head large, anterior margin oblique, defined by sharp, ventrally-projecting process, ventral keel toothed anteriorly. Antenna 1, article 1 of peduncle enlarged; antenna 2 attached well behind eye. Maxilliped, palp article 4 elongate. Gnathopod 2, coxa greatly enlarged, serrate anteriorly, expanded posteriorly, with sinuous ventral margin; carpus shortened; propodus inflated, palm oblique, with 6 major teeth; dactyl long, recurved, apex bifid.

Description. Head, lateral margins rounded, anterior margin oblique, defined by sharp ventral process, eye small relative to head size, composed of approximately 10 ommatidia, ventral keel a broad, toothed projection extending below margin of head. Antenna 1, 1.38 times length of head to posterior margin of pereonite segment 4; article 1 enlarged, articles 1–3, 29:15:10, flagellum subequal to peduncle, 9-articulate. Antenna 2, 0.89 times the length of head to pereonite 4; flagellum short, 3- to 5-articulate. Maxilliped, palp article 4 very elongate, 1.95 times length of palp article 3. Gnathopod 2, coxa enlarged, greatly exceeding coxae 3–4; carpal process shortened, propodus inflated, palm oblique, with 6 major teeth separating major indentations; dactyl elongate, recurved, reaching near

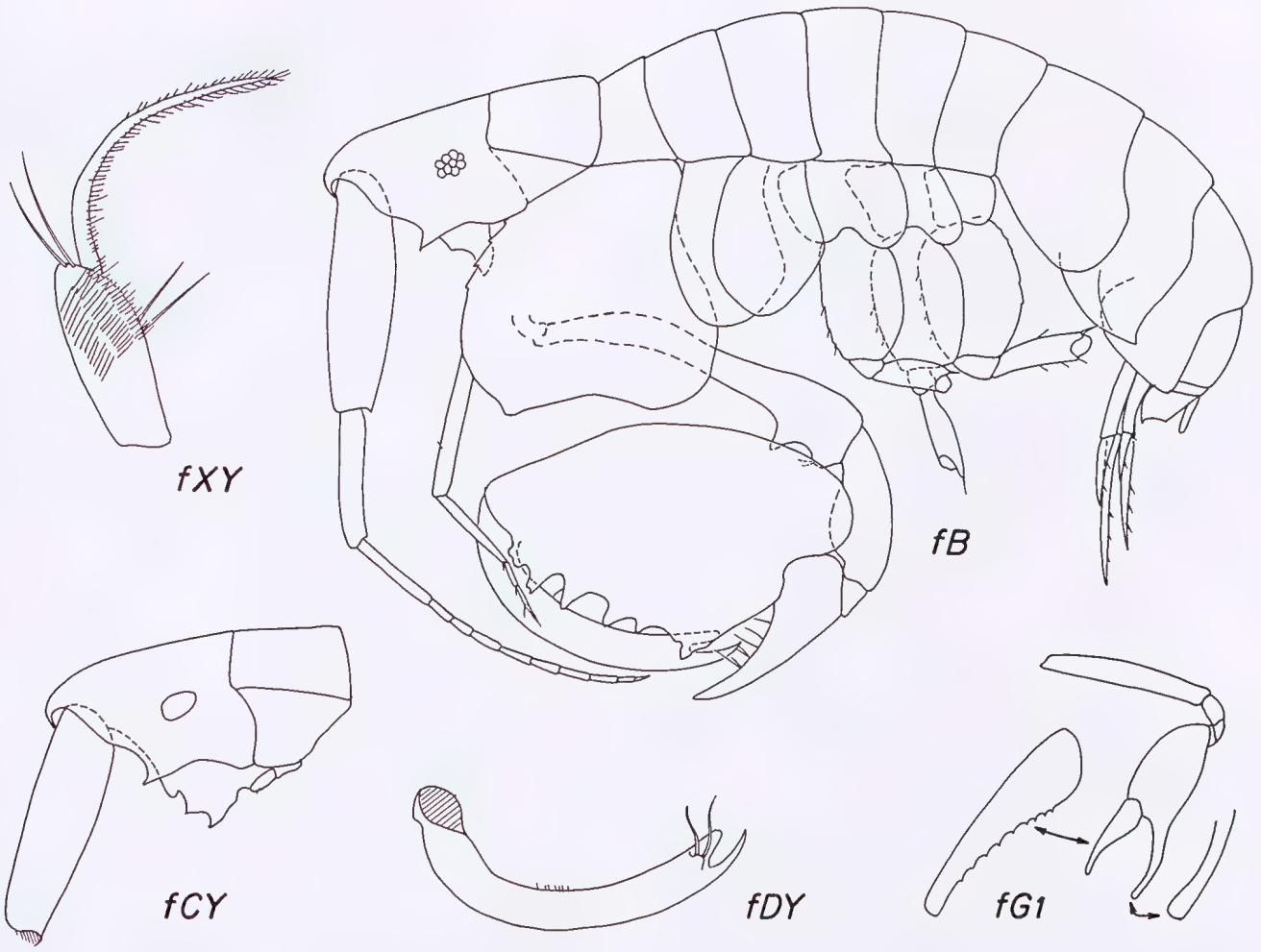

Fig. 6. *Anamixis falarikia*, anamorph male "F".

mid-region of carpus, apex bifid. Uropod 3 missing. Telson apically rounded.

Relationship. *Anamixis falarikia* resembles *A. papuaensis* in the enlarged coxa 2 and aberrant palm of gnathopod 2. *Anamixis falarikia* resembles *A. excalibur* in the enlarged first peduncular segment of antenna 1 and in the elongate palp article 4 of the maxilliped. *Anamixis falarikia* differs from *A. excalibur* in the more oblique head angle and ventrally projecting process; in the dominance of coxa 2; in having gnathopod 2 with a shortened carpal process, inflated propodus with oblique, 6-toothed margin; and in the bifid apex of the dactyl.

Remarks. This remarkable specimen is known from the original description from the type locality.

Habitat. Coral reefs, algal covered coral rubble.

Distribution. Pacific Ocean, Ifaluk Atoll, Caroline Islands, 0–1 m.

Anamixis hansensi Stebbing, 1897

Fig. 7

Anamixis hanseni Stebbing, 1897: 36–38, fig. 11; 1906: 170–171, fig. 42–43.

Diagnosis. Head angle oblique, lacking any defining cusps; anterior margin of ventral keel with microscopic teeth; gnathopod 2 with terminal setae; coxa 2 enlarged, broadly rounded, margin smooth; propodus of gnathopod 2 elongate, 3.05 times deeper than wide, with 3 teeth; dactyl with 2 slight projections on inner margin.

Description. Head, lateral margin rounded, anterior margin oblique; antenna 1, ratio of segments 1–3, 32:25:14; eyes compact, large, composed of numerous ommatidia, ventral keel projecting as truncate process, with anterior microscopic teeth and excavate bottom margin, anteroventral corner defined by small, sharp projection; maxilliped, article 4, 1.25 times article 3. Antenna 2 attached near posterior margin of eye. Gnathopod 2, coxa larger than 3–4, margins smooth;

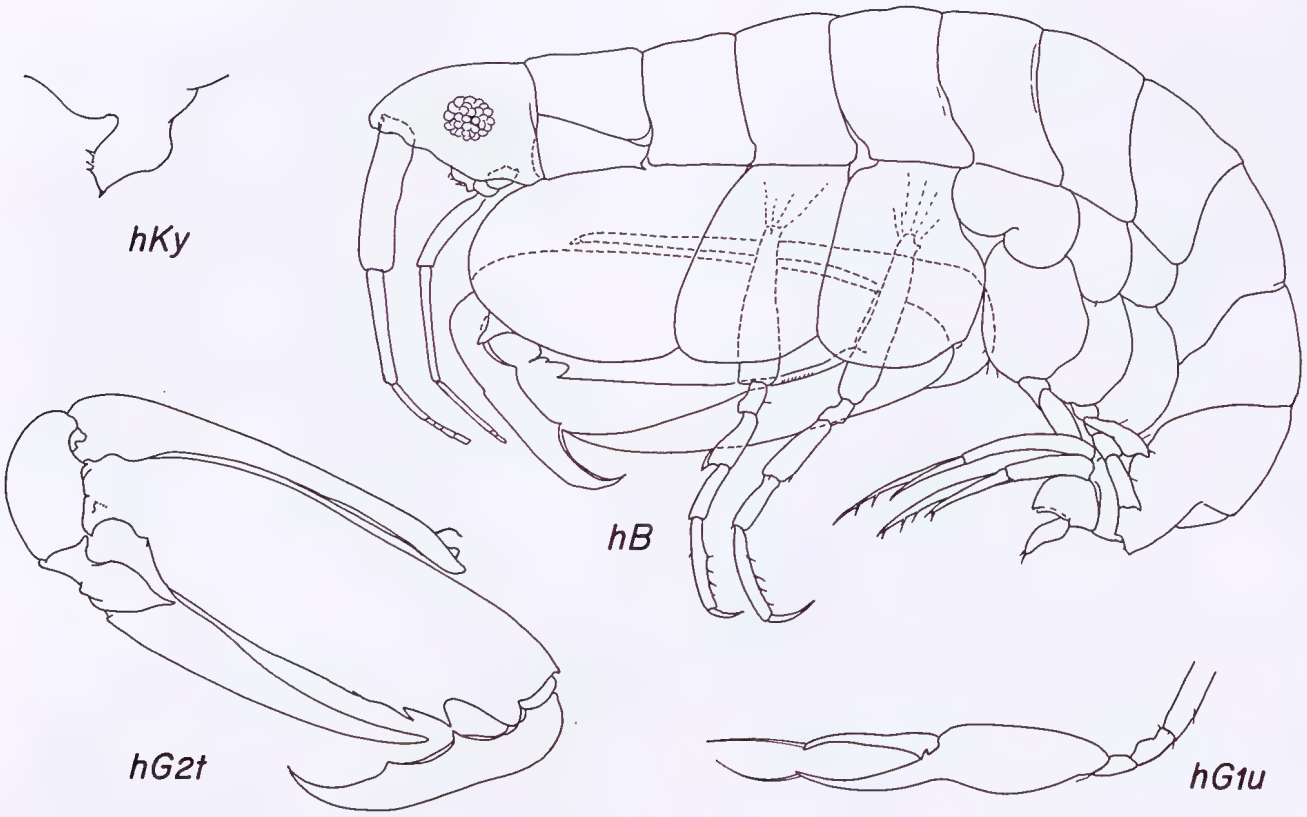

Fig. 7. *Anamixis hanseni*, anamorph male "H".

carpus elongate; propodus very elongate, with 3 major teeth; dactyl with 2 small projections in inner margin. Coxa 3 smaller than 4, both with smooth margins. Uropod 3 missing. Telson apically rounded, 1.28 times longer than wide.

Relationship. *Anamixis hanseni* is most closely related to *A. cavatura* but differs from this species in the following characters: the oblique head angle lacking any defining process; the smooth margins of coxa 2; in gnathopod 2, the elongate propodus with 3 teeth, and dactyl with two small projections on the inner surface. It differs from *A. vanga* in lacking the laterally excavate margins of the head, the apically produced ventral keel with microscopic teeth, smooth margins on coxa 2, and the elongate propodus of gnathopod 2.

Remarks. In the past, this author has confused this species with *A. cavatura* (Thomas, 1979; Thomas & Taylor, 1981; Thomas & Barnard, 1983). A loan of the type specimen was requested from the Copenhagen Museum to confirm specific characters, but unfortunately the head was missing. Thus, minute details of head margins and ventral keel cannot be discerned. However, Stebbing's excellent original description clearly sets this species apart from *A. cavatura*.

Habitat. Stebbing lists *A. hanseni* as collected from the coral *Goniastraea varia*, which is not a valid specific name for the genus. In addition, *Goniastraea* is not a Caribbean coral but rather an Indo-Pacific genus. It is the author's suspicion that the coral may have been misidentified by the original collector, J.H. Hansen. A more remote possibility is that the name of the coral is correct and the collecting locality is incorrect and may in fact not be in the Tropical Atlantic as depth, specific location, and other collecting particulars remain unknown.

Distribution. Tropical Atlantic, West Indies (no specific location given by Stebbing in his description, but reported to possibly be St. Croix, J. Stock, personal communication).

Anamixis jebbi n.sp.

Figs 8,9

Type material. HOLOTYPE, anamorph male "A", 2.54 mm, USNM 253745, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of cemented rubble in centre of reef, 1–2 m, J.D. Thomas, 28 February 1990, JDT-PNG-67; 1 PARATYPE, anamorph male, "C", USNM 253746, 2.50 mm, overturned and partially cemented *Acropora cytherea* rubble, 2–3 m, J.D. Thomas, 10 February 1990, JDT-PNG-40; 2 PARATYPES, leucomorph male "D", 1.92 mm, USNM 253747, leucomorph female "E", 1.62 mm, USNM 253748, and 5 other unmeasured leucomorphs, USNM

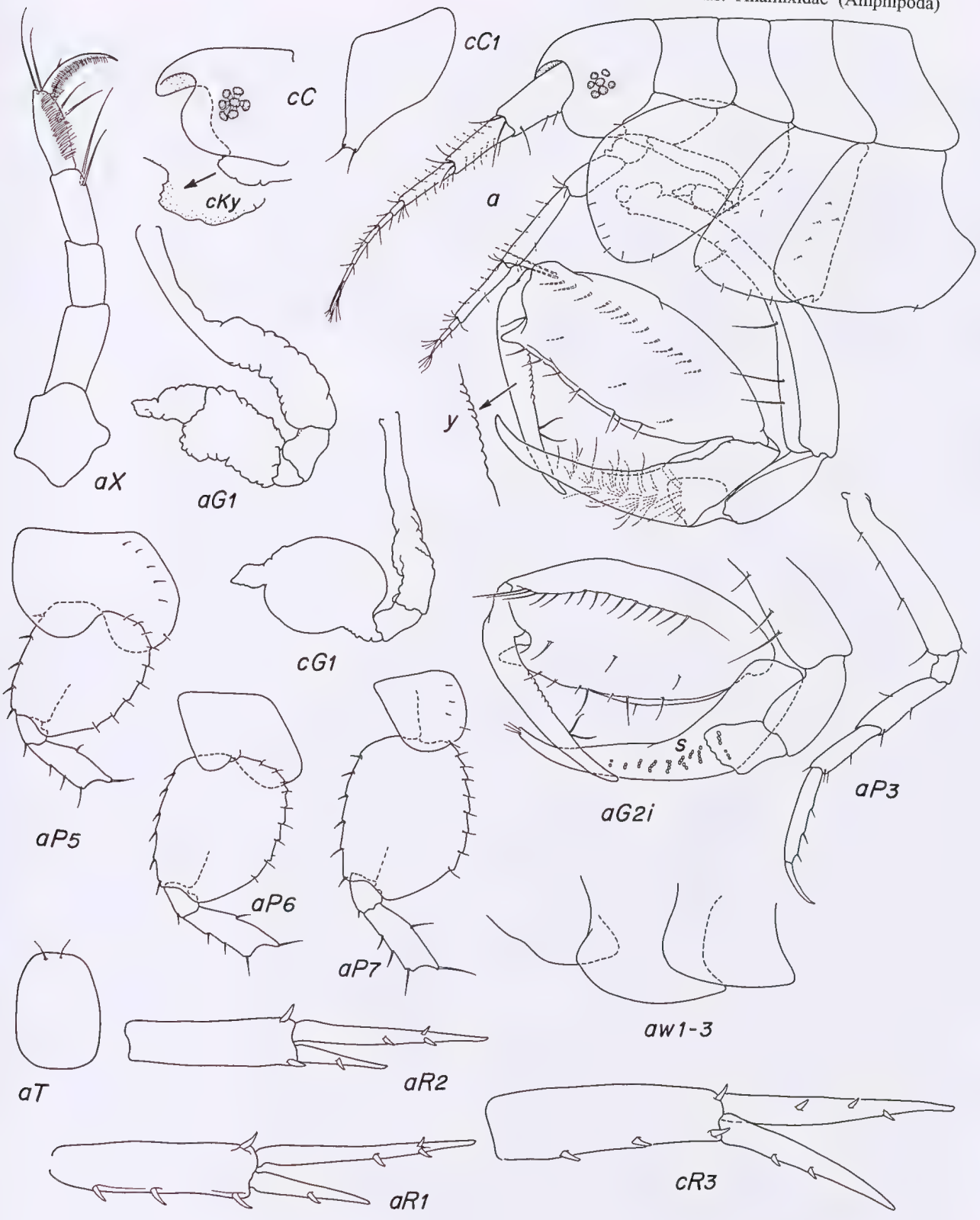

Fig. 8. *Anamixis jebbi* n.sp., holotype, male, 56 "A", 2.75 mm; "C", anamorph male, 2.50 mm.

253749, and 3 unmeasured anamorphs, USNM 253750, Padoz Tinan reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of overturned plates of *Acropora cytherea* 3 m, J.D. Thomas, 15 February 1990, JDT-PNG-46; 4 PARATYPES, 3 anamorphs and 1 leucomorph, USNM 243313, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, heavily cemented rubble from centre of reef, 1 m, J.D. Thomas, 18 February 1990, JDT-PNG-50a,b; 2 PARATYPES, 1 anamorph and 1 leucomorph, USNM 243314, Guzem reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of *Acropora* rubble, 2.5 m, J.D. Thomas, 12

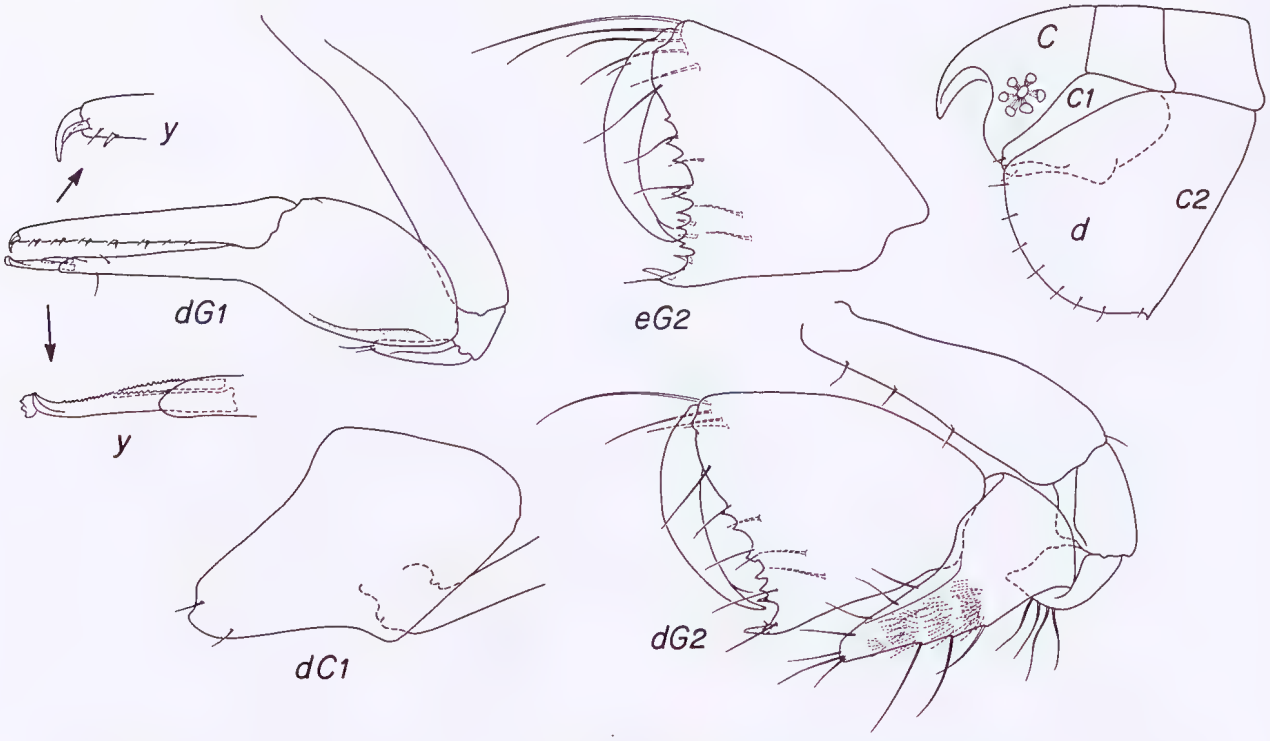

Fig. 9. *Anamixis jebbi* n.sp., "D", leucomorph male, 1.92 mm; "E", leucomorph female, 1.62 mm.

February 1990, JDT-PNG-44a; 2 PARATYPES, 1 anamorph and 1 leucomorph, USNM 243315, Tab Anchorage, Madang, Papua New Guinea, patch reef bearing 210° from Wongad Island, rubble from 3 m, J.D. Thomas, 13 February 1990, JDT-PNG-45a.

Diagnosis. Gnathopod 1 vestigial, persisting in post-transformation anamorphs as minute fleshy appendage; eyes reduced, composed of 7 ommatidia in both anamorph and leucomorph stages. Ventral keel rounded, anterior margin with two small cusps. Gnathopod 2, basis with 3 long setae anteriorly; carpus projecting above attachment with ischium, proximolateral margin weakly serrate; propodus with long line of mediofacial feeding setae near anterior margin and, a second, posterior row composed of 3 widely spaced setae.

Description. Head margin broadly rounded, lacking any defining processes; ventral keel rounded, sinuous, anterior margin cuspate; eyes reduced, bearing 7 scattered ommatidia. Antenna 1, ratio of segments 1–3, 15:12:11, peduncle segment 2 and 3 with 5–6 pairs of setae each; flagellum 6-articulate, articles 5 and 6 with aesthetascs. Antenna 2, flagellum short, 4-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.1 times length of article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1, coxa apically bifid, bearing 2 small setae; remainder of appendage extremely reduced, remaining wrinkled and fleshy, and persisting in subsequent post-transformational moults. Gnathopod 2, coxa scarcely larger than 3 or 4, evenly rounded, bearing approximately 6 submarginal setae; basis with 3 long setae along anterior margin; carpus slightly recurved, vaulting above attachment of ischium, lateral ridge weakly serrate from midpoint; propodus with double row of mediofacial feeding setae, anterior row 70 per cent of propodus, posterior row composed of 3 widely spaced setae; dactyl straight, inner surface margin nodulose proximally, paired setae inserted toward apex. Pereopod 3, coxa subrectangular, anterior and posterior margins straight, defined by small cusp, ventral margin furnished with 3–4 submarginal setae, mediofacial surface with scattered small setulae; remainder of pereopod normal. Pereopod 4, coxa equal to or slightly larger than 2, posteroventral margin expanded distally, ventral margin with small posterior indentation, anterior margin with several small mediofacial setulae; remainder of pereopod similar to pereopod 3. Pereopods 5, coxa bilobed, posterior margin with 6 submarginal setae; basis suboval, anterior margin spinose, posterior margin with series of indentations, each bearing a single seta; remainder of pereopod missing. Pereopod 6, coxa bilobed, relatively smaller than coxa 5; articles 5–7 missing; remainder of articles similar to pereopod 5. Pereopod 7, coxa entire, posterior margin with single posterior seta, medial surface furnished with several small setulae; articles 5–7 missing. Epimera normal for genus. Outer rami of uropods 1 and 2 shortened, approximately 50 per cent of inner ramus. Uropod 3, outer ramus 85 per cent of inner ramus. Telson 1.3 times longer than wide; bearing 2 apical, and two pairs of dorsofacial setae.

Leucomorphs. Description of male leucomorph "D": head, margin rounded, eyes with seven scattered ommatidia. Gnathopod 1, coxa reaching ventral margin of head, apically rounded and bearing 2 setae; carpus, inner margin bare, apex with 2 serrate spines, the larger spine 1.8 times longer than the shorter and bearing a

vertical terminal flake or blade; propodus, finely denticulate and furnished with a series of paired small spines and setae, dactyl possibly represented at apex by short hook. Gnathopod 2, coxa rounded, ventral margin expanded, bearing 8 submarginal setae, posterior margin defined by small cusp; second article with 3 anterior setae; palm of propodus more or less transverse, palmar margin defined by series of sharp cusps and 4 large embedded spines, corner of palm not produced forward; dactyl reaching next to last embedded palmar spine. Leucomorph female "E" similar to male except for a relatively smaller second gnathopod. Palm of female gnathopod 2 slightly excavate, hind margin tapering; dactyl not reaching next to last embedded palmar spine.

Etymology. Named for Matthew Jebb, Director, Christensen Research Institute in Madang, whose enthusiastic support of our amphipod biodiversity project and untiring good humour has made our efforts in Papua New Guinea most rewarding.

Relationship. *Anamixis jebbi* does not appear to share close affinities with any other known anamixid. The small, vestigial first gnathopod that persists in post-transformational anamorphs is unique and suggests an evolutionary link to *Paranamixis* where gnathopod 1 has been lost in post-transformational moults, but persists as a tiny vestige in transformational anamorphs. Until additional material of a variety of *Paranamixis* species are available for dissection and detailed observation, the fused inner plates of the maxilliped place *A. jebbi* in *Anamixis*. *Anamixis jebbi* also has an unusual attachment of the carpus to the ischium, with the attachment being significantly further down the carpus than is exhibited in other taxa. Articles 2 and 3 of antenna 1 are unusually setose for an anamixid, and few other taxa have such a long row of feeding setae on the medial surface of gnathopod 2. Because the second gnathopods and antennae are used in conjunction with the maxilliped in feeding, these unusual features may be attributable to a different feeding ecology than is found in other species. The variable form and surface texture of gnathopod 1 probably results from preservation procedures. Leucomorphs of *A. jebbi* are readily separated from other species by the reduced (and seemingly consistent) number of ommatidia, 7, and, in fresh material, by the pale pinkish colour.

Remarks. Colour of freshly preserved anamorphs and leucomorphs a pale, translucent pink, fading rapidly in preservative.

Habitat. Specific habitat or host is unknown, but specimens of *A. jebbi* were always collected from deep within rubble accumulations, indicating a preference for highly cryptic habitats. The reduced number of ommatidia also suggest a cryptofaunal existence and low ambient light conditions.

Distribution. Bismarck Sea, shallow coral reefs in the Madang region of Papua New Guinea, 1–3 m.

Anamixis kateluensis n.sp.

Fig. 10

Anamixis stebbingi J.L. Barnard, 1965: 488–489, fig. 4.

Type material. HOLOTYPE, anamorph male "K", 1.98 mm, USNM 106914, Caroline Islands, Katelu area of south-west Falarik Islet, wash from algae growing on dead coral, 25 m from shore, 0–1 m, D.P. Abbott, 21 October 1953, 145-C-2.

Diagnosis. Antenna 2 shorter than antenna 1, reaching only 0.69 on antenna 1; ventral keel large, tapering posteriorly, ventral margin defined by sharp, vertical tooth; gnathopod 2, coxa 2 apically produced, with slight anterior and posterior emarginations; gnathopod 2, propodus with subdistal indentation near base of dactyl; coxa 3 slightly larger than 2 or 4, anterior margin expanded, posterior margin tapering; coxa 4, posterior margin tapering.

Description. Holotype "K". Head, anterior margin transverse, corner defined by small upturned cusp, eye with 16 ommatidia. Antennae: antenna 1, ratio of segments 1–3, 15:11:8; flagellum 8-articulate; antenna 2, shorter than 1, apex reaching articles 5–6 on flagellum of antenna 1, flagellum 4-articulate. Maxilliped, inner plates with small apical cleft; outer plates lacking inner lobes; palp article 4 missing. Gnathopod 1, opposing chelae recurved and crossing on closure, apices slightly bulbous; article 6 with toothed inner margin. Gnathopod 2, coxa slightly smaller than 3; basis unadorned with setae or spines; carpal lobe thickened, straight, tapering evenly to apex, distal portion with small subapical swelling, apex reaching end of propodus; palm unexpanded, hindmargin slightly excavate, adjacent to small subdistal cusp; dactyl with elevated truncate projection near base, inner margin with small process bearing paired setae, remainder smooth. Coxa 3, slightly larger than 2 or 4, anterior margin expanded. Coxa 4 smaller than 2 or 3, posteroventral margin oblique. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, submarginal setae present. Pereopod 7, coxa entire, ovate. Uropods 1–2, outer rami shortened, approximately one-half of inner rami. Uropod 3 missing. Telson apically rounded.

Leucomorphs. Unknown.

Etymology. Named for the Katelu area of south-west Falarik, Ifaluk, the type locality.

Relationship. *Anamixis kateluensis* closely resembles *A. bazimut* from Papua New Guinea and *A. moana* from Hawaii in the transverse margin of the head, the broad and enlarged ventral keel, the apically notched inner plates of the maxilliped and in the long, non-geniculate carpal lobe and similar propodus of gnathopod 2. *Anamixis kateluensis* differs from both *A. bazimut* and *A. moana* in the relatively shorter antenna 2; the more

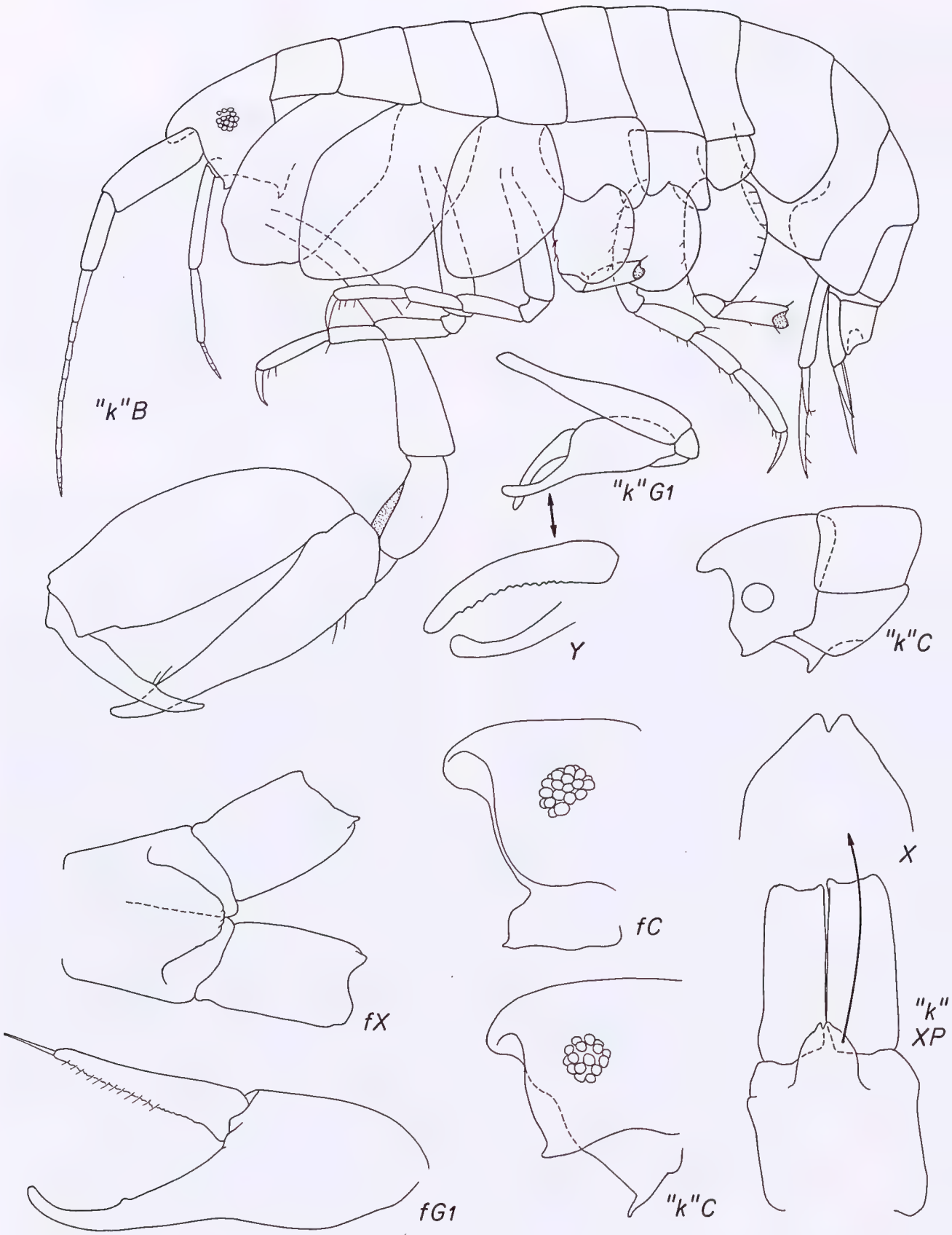

Fig. 10. *Anamixis kateluensis* n.sp., holotype, anamorph male "K", 1.98 mm. *Anamixis pacifica*, anamorph male "F", 5.87 mm.

oblique ventral keel; the expanded anterior margin of coxa 3; and in having coxa 2–4 of differing morphology and size. Based upon examination of the original specimen, the second gnathopod of *A. kateluensis* also exhibits several minor features not found in *A. moana* or *A. bazimut*: a relatively straighter carpal lobe with a slight swelling on the inner margin near the apex and the presence of a subdistal cusp on the palm.

Remarks. Barnard (1965) reported this species as *A. stebbingi*, but his description and drawings were adequate to establish significant character differences found in this species. Examination of Barnard's figured specimen confirmed the specific differences.

Habitat. From coral rubble, assumed to be commensal.

Distribution. Central Pacific Ocean, Ifaluk Atoll, Falarik Island, Caroline Islands, 0–1 m.

Anamixis mahe n.sp.

Fig. 11

Type material. HOLOTYPE, male "A", 2.66 mm, USNM 243316, rubble and stones among algal turf in current-swept channel, sheltered embayment near Mahe Beach Motel, Mahe, Seychelles, 0.5 m, J. Clark, 29 April 1984, J-Sey-2; 1 PARATYPE, male "B", 2.56 mm, 243317, J-Sey-2.

Diagnosis. Anterior margin of head transverse, defined by small cusp; anterior margin of ventral keel denticulate. Gnathopod 1, carpus with geniculate apical seta; propodus with one geniculate and one straight seta apically. Gnathopod 2, lateral margin of carpus bifid near apex, proximal margin serrate; dactyl elongate, recurved; anterior margin of coxae 3–4 oblique.

Description. Head, anterior margin transverse, anteroventral corner defined by small cusp; antenna 1, first peduncular segment scarcely exceeding articles 2 and 3; ratio of articles 1–3, 15:14:13; ventral keel rounded, barely projecting below margin of head, anterior surface with 3–4 irregular projections, posterior margin evenly rounded; eye with 18–20 ommatidia; accessory flagellum a minute scale with 2 apical setae; flagellum 9-articulate, aesthetascs on articles 6–8. Antenna 2 normal for genus; fifth peduncular article with long seta; flagellum short, 5-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.3 times length of article 3. Coxae 2–4 subequal in size. Pereonite 1 with prominent lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, anteroventral margin rounded and bearing 2 apical setae; carpus, recurved apically, bearing a single geniculate seta, inner margin smooth; propodus, inner margin finely serrate with embedded short setae, bearing one geniculate, and one straight seta apically. Gnathopod 2, coxa subequal to 3 and 4 in size, 1.70 times deeper than wide, evenly rounded, bearing 2–3 small setulae and defined by a small cusp at the posteroventral margin; basis unarmed, with 3 short setae along anterior margin; carpus with prominent bifid process at Mark 0.77, with 3 small setulae, lateral ridge with irregular serrations on proximal portion; propodus, hind margin with 6 short setae, distal margin excavate, lacking sharp cusps or teeth, medial surface with row of 10–12 long feeding setae; dactyl long and recurved, inner margin smooth, 2 setae present on inner margin. Pereopod 3, coxa 1.5 times deeper than wide, anteroventral margin slightly excavate, posteroventral margin with small cusp, small setulae present along ventral margin; remainder of pereopod normal for genus. Pereopod 4, coxa 1.2 times deeper than wide, projecting midventrally, posteroventral margin defined by rounded process, small setulae along ventral margin; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed; basis spinose anteriorly, posterior margin evenly rounded with small submarginal setulae. Pereopod 6, coxa bilobed, posterior lobe much deeper than anterior; basis spinose anteriorly, posterior margin evenly rounded with small submarginal setulae. Pereopod 7, coxa entire, bearing a single posterior seta; basis spinose anteriorly, posterior margin with small serrations, each with small setule. Uropods 1 and 2, outer rami about half the length of the inner. Uropod 3 missing. Telson subquadrate, 1.5 times longer than wide, apical margin rounded with two setulae, dorsal surface bearing two pairs of double setulae.

Etymology. Name refers to the type locality Mahe, in the Seychelles.

Relationship. *Anamixis mahe* is the only anamixid from the Pacific and Indian Oceans that bears long apical setae on gnathopod 1, this character being previously restricted to Caribbean *Anamixis*. *Anamixis mahe* is related to *A. barnardi* in having a rounded ventral keel, bifid distal process on the carpus of gnathopod 2, and in having coxa 4 emarginate ventrally. *Anamixis mahe* differs from *A. barnardi* in having an apically setose carpus and propodus on gnathopod 1, and a more quadrate telson. *Anamixis stebbingi* also has an emarginate ventral margin on coxa 4. Both *A. barnardi* and *A. stebbingi* have a serrate proximal ridge on the medial margin of the carpus on gnathopod 2, whereas *A. mahe* exhibits this character on the lateral margin of the carpus. The denticulate anterior margin of the ventral keel of *A. mahe* resembles the condition seen in *A. jebbi* from Papua New Guinea.

Leucomorphs. Unknown.

Remarks. Leucomorphs of *A. mahe* are undocumented.

Habitat. Specific host(s) or habitat(s) unknown, general habitat is shallow algal turf in coral reef rubble zones.

Distribution. Indian Ocean, Mahe, Seychelles.

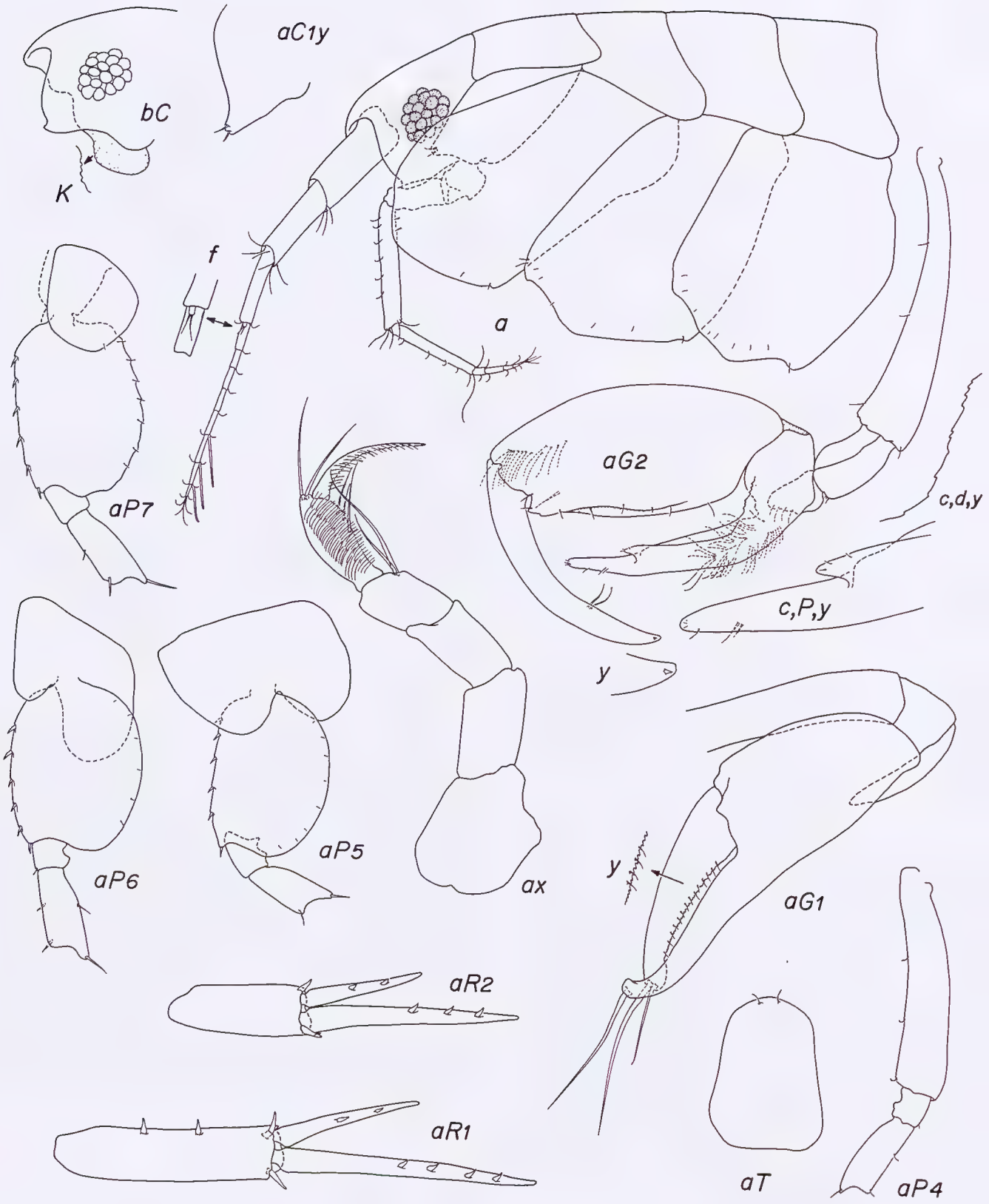

Fig. 11. *Anamixis mahe* n.sp., holotype, anamorph male "A", 2.66 mm; "B", anamorph male, 2.56 mm.

Anamixis moana n.sp.

Fig. 12

Anamixis stebbingi Barnard, 1970: 64, fig. 27.

Type material. HOLOTYPE, anamorph male "M", 2.40 mm, BPBM 58650, heads of *Pocillopora meandrina*, 2 m, Sampan Pass, Kaneohe Bay, Oahu, divers Kruschwitz and Bowers, 23 Feb. 1967, JLB Haw 10.

Diagnosis. Anterior margin of head transverse, with or without cusp; ventral keel large, oblique, projecting well below ventral margin of head, anteroproximal margin parallel to anterior margin of head, anterodistal and posterior margins oblique, tapering to broad, ventrally directed triangular process beneath eye; maxilliped inner plates fused, apically subtruncate, coxae 2–4 subequal in size, ventral margin of coxa 2 slightly expanded, angular, anteroventral and posteroventral corners smooth, 3 and 4 not expanded ventrally.

Description. Holotype "M". Head, anterior margin transverse, sometimes with small cusp. Antennae: antenna 1, ratio of articles 1–3, 12:8:6; flagellum 4- or 5-articulate; antenna 2 barely shorter than 1; flagellum 3- or 4-articulate. Eyes with approximately 17 loosely packed ommatidia, ventral keel massive, anteroproximal margin vertical, anterodistal margin oblique, tapering posteriorly to a broad triangular projection beneath eye. Maxilliped inner plates fused, subtruncate; outer plates lacking inner lobes; article 4 of maxilliped 1.6 times longer than article 3. Gnathopod 1 carpochelate, apex of article 5 slightly bulbous. Gnathopod 2, coxa with angular midventral projection; carpal lobe thick, elongate, reaching almost to end of propodus, apex blunt, slightly recurved; propodus slightly expanded, lacking any significant teeth or cusps. Pereopods 3–4 similar, ventral margins of coxae linear. Pereopods 5–6 similar, coxae bilobed. Pereopod 7, coxa entire, oval. Uropods 1–3, outer rami of 1 and 2 shortened to one-half of inner; of uropod 3, two-thirds. Telson entire, broad, apically rounded, 1.3 times longer than wide.

Leucomorphs Unknown.

Etymology. From the Hawaiian "moana", meaning ocean.

Relationship. *Anamixis moana* appears most closely related to *A. kateluensis* from Micronesia and *A. bazimut* from Papua New Guinea in the large ventral keel, subequal coxae 2–4, and general morphology of gnathopod 2. *Anamixis moana* differs from both *A. kateluensis* and *A. bazimut* in having the inner plates of the maxilliped apically truncate. *Anamixis kateluensis* differs from *A. moana* in having shorter second antenna; a more oblique ventral keel with distoventral projection; in various features of gnathopod 2; in having an expanded anterior margin of coxa 3; and in having coxae 3–4 with ventral margins not tapered. *Anamixis bazimut* has a vertical anterior margin on the ventral keel; an angular expansion on the ventral margin of coxa 2, and virtually straight hindmargin of gnathopod 2 propodus.

Remarks. Collecting from intermediate locations may provide additional information on the distribution and variation among the clade to which *A. bazimut* belongs. All members of this clade appear to be relatives of a previously widespread palaeoendemic that may have subsequently given rise to numerous species as ancestors became isolated in island archipelagos. Representative collections of amphipods from reef systems in the Central and South Pacific are limited, but additional collecting efforts in isolated island areas are sure to provide a wealth of new anamixid species.

Habitat. Coral rubble, specific host(s) unknown.

Distribution. Hawaiian Islands, coral rubble, 2–30 m.

Anamixis nedcampensis n.sp.

Fig. 13

Type material. HOLOTYPE, anamorph male "L", 3.02 mm, AM P41033, green and brown algae, inshore limestone reef south of Ned's Fish Camp, Ningaloo Reef, Cape Range National Park, Western Australia, 21°59'S 113°55'E, 1 m, R.T. Springthorpe, 2 January 1984, WA-373. PARATYPES, anamorph males "C" 2.95 mm; "M" 2.87 mm.

Diagnosis. Article 5 of gnathopod 1 distally dilated. Gnathopod 2, carpus with distal bifid process; propodus narrow, hindmargin straight, smooth, anterior margin not expanded.

Description. Holotype "L". Head, anterior margin transverse, anteroventral corner with small cusp; ventral keel rounded; eyes with 16 compact ommatidia. Antennae: antenna 1, peduncular ratio 23:18:12; accessory flagellum minute, 1-segmented; flagellum 10-articulate. Antenna 2, flagellum short, 4- or 5-articulate. Maxilliped, inner plates fused into apically rounded process bearing 2 nipple-like processes, outer plates lacking inner lobes; palp article 4, 1.2 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 distally dilated; article 6 geniculate, inner margin with few weak serrations. Gnathopod 2, coxa subequal to 3 and 4, anterior margin with small cusp, ventral margin rounded; carpus with distal bifid process; propodus, hindmargin smooth, sparsely setose, anterior margin straight; dactyl long, slightly recurved, with paired distomedial setae. Pereopod 3, anteroventral of coxa margin defined by moderate cusp, ventral margin slightly expanded. Pereopod 4, anteroventral margin of coxa

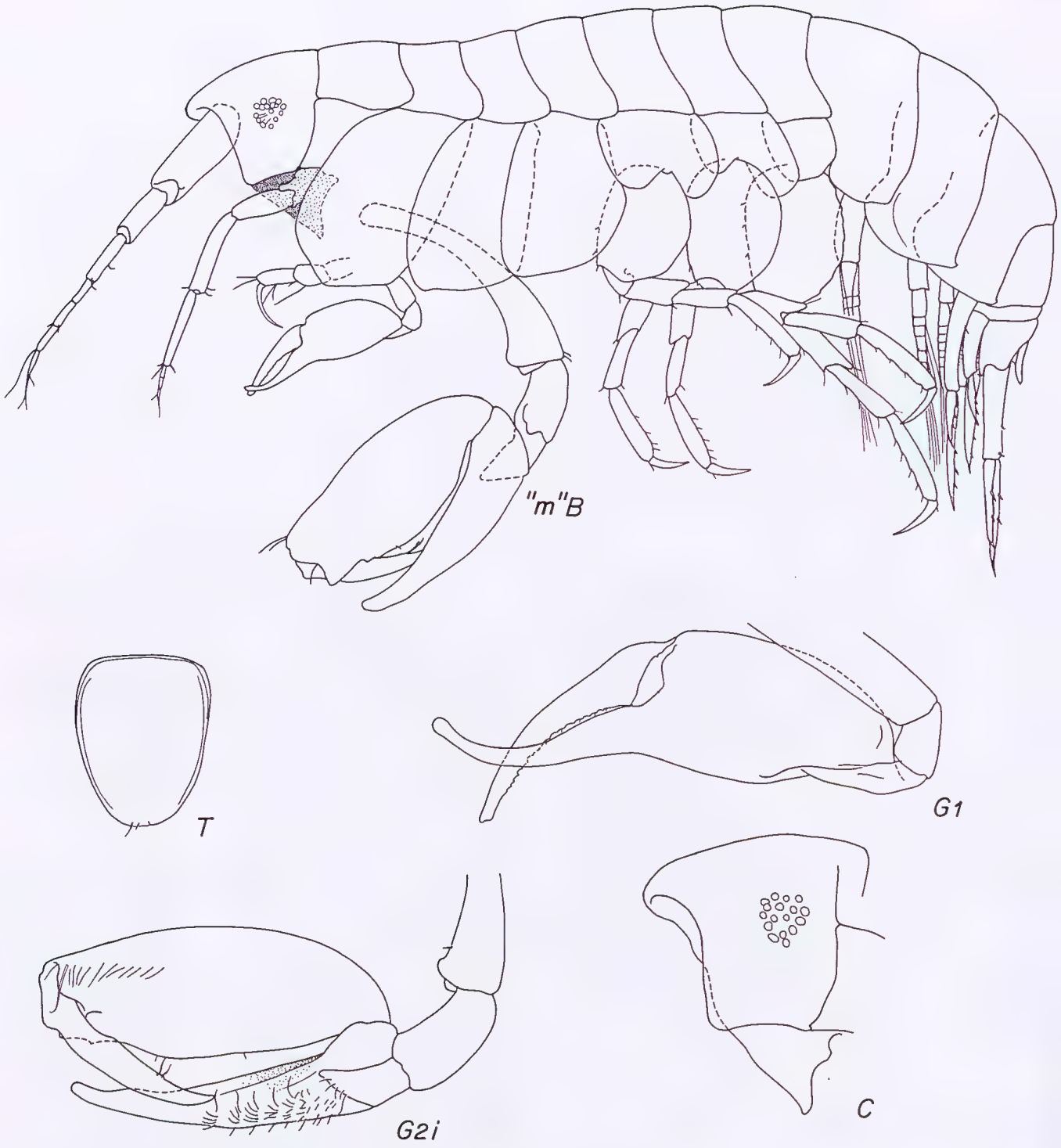

Fig. 12. *Anamixis moana* n.sp., holotype, anamorph male "M".

defined by moderate cusp, ventral margin expanded, crenulate, posterior margin slightly expanded. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin evenly rounded and furnished with 6–9 submarginal setae. Pereopod 7, coxa entire, with single posteroventral seta; basis spinose anteriorly, posterior margin ovorectangular, ventral margin produced along article 4. Uropods 1 and 2, outer rami one-half length of inner. Uropod 3 missing. Telson entire, broad, 1.2 times longer than wide, with two groups of paired dorsofacial setae, distal margin with pair of apical setae.

Leucomorphs. Unknown.

Etymology. Named for Ned's Fish Camp, a popular camping area near Ningaloo Reef, Western Australia.

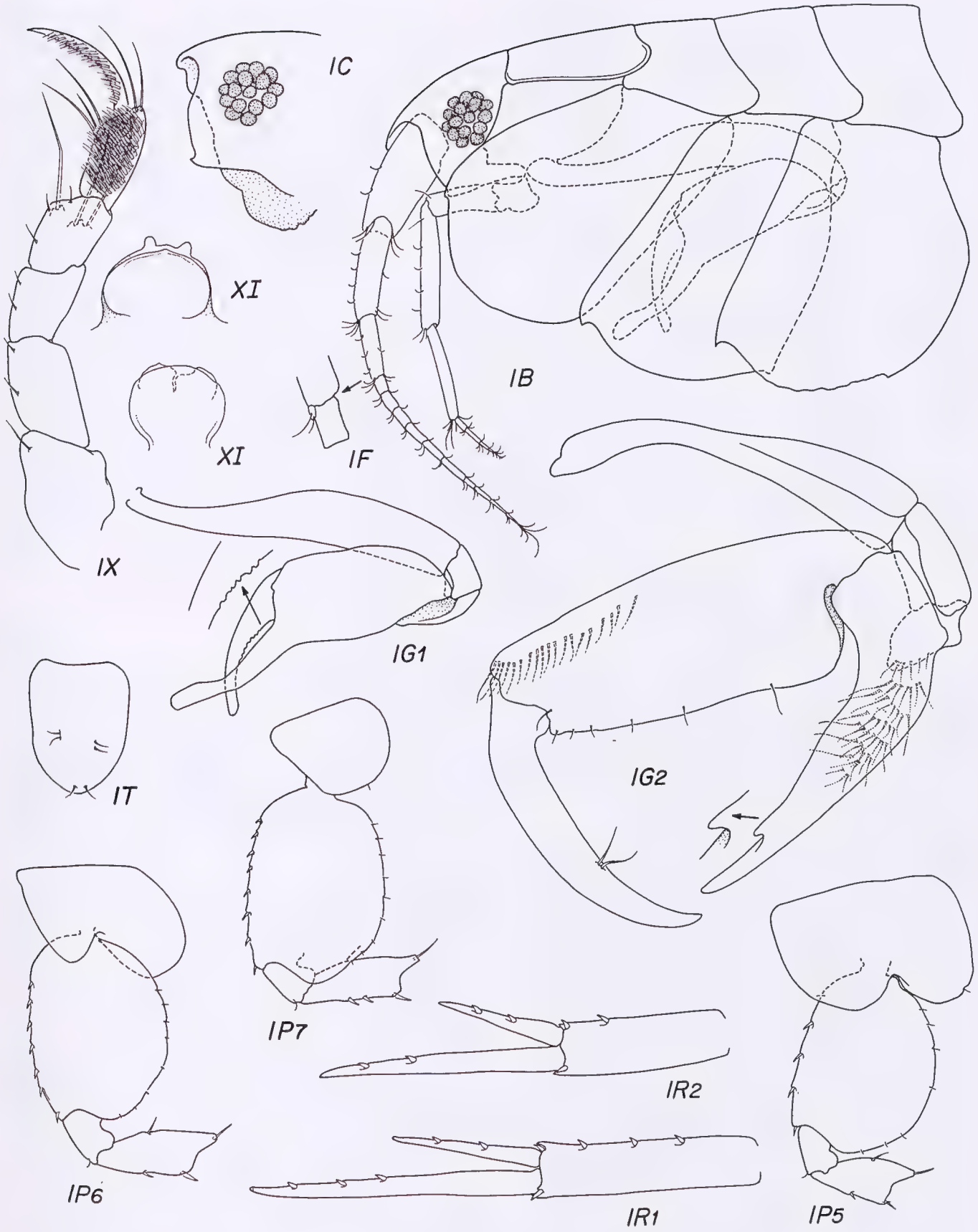

Fig. 13. *Anamixis nedcampensis* n.sp., holotype, anamorph male "L", 3.02 mm; "C", 2.95 mm; "M", 2.87 mm.

Relationship. *Anamixis nedcampensis* is part of a triad of Indian Ocean species, (*A. nedcampensis, A. mahe, A. barnardi*), of anamixids having a rounded ventral keel; subequal coxae 2–4, and in having gnathopod 2 with a bifid process on the carpus, and an elongate, unarmed dactyl. The lack of a serrate proximal ridge on the carpus of the second gnathopod further distinguishes *A. nedcampensis* from *A. barnardi* and *A. mahe*.

Remarks. Superficially, *A. nedcampensis* most closely resembles *A. mahe* and *A. barnardi* in the bifid process on the carpal lobe of gnathopod 2. However, *A. nedcampensis*, and all other Indo-Pacific anamixids differ from *A. mahe* in lacking terminal setae on gnathopod 1. The other Indian Ocean anamixid, *A. stebbingi*, lacks an apically dilated article 5 of gnathopod 1, and has a serrate carpal lobe, and a denticulate inner margin on the dactyl of gnathopod 2.

Habitat. Presumed commensal, specific host(s) unknown, general habitat shallow limestone reefs among algae.

Distribution. Eastern Indian Ocean, Western Australia, coral reefs, 1 m.

Anamixis ningaloo n.sp.

Fig. 14

Type material. HOLOTYPE, anamorph male "W", 2.63 mm, AM P41031, inside outer reef off Ned's Fish Camp, Ningaloo Reef, Cape Range National Park, Western Australia, 21°59.5'S 113°54.5'E, 2 m, airlift from living *Acropora* sp., R.T. Springthorpe and J.K. Lowry, 1 January 1984, station WA-346.

Diagnosis. Antenna 1, peduncle article 1 enlarged. Gnathopod 1, article 5 thin and attenuate relative to article 6. Gnathopod 2, coxa not greatly enlarged, anteroventral and posteroventral corners each defined by a single cusp, ventral margin expanded; carpal lobe of moderate length, thickened; ventral margin of propodus oblique, defined by a tooth and a truncate process; dactyl inflated, inner margin with denticulate proximal process and smaller distal process bordered by paired setae.

Description. Holotype "W". Head, anterior margin transverse, anteroventral corner defined by small cusp; ventral keel, anterior margin oblique, bearing 3 small teeth on anterodistal margin, ventral margin defined by anteroventral tooth; eyes with 15 loosely bundled ommatidia. Antennae: antenna 1 peduncular ratio 35:25:17; article 1 enlarged, 2.1 times thicker than article 2; flagellum 10-articulate, aesthetascs on articles 3–10; antenna 2 apex reaching to flagellar article 4 of antenna 1, flagellum short, 4-articulate. Maxilliped, inner plates fused into apically rounded process with slightly sinuous anterior margin; outer plates lacking inner lobes; palp article 4, 1.6 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 feeble, distally attenuate; article 6 straight, inner margin with complexly serrate inner margin, apical pore present. Gnathopod 2, coxa scarcely larger than 3 or 4, ventral margin expanded, defined by cusp at anterior and posterior margins; carpus thickened, unarmed, 0.85 the length of propodus, hindmargin smooth, ventral margin oblique, defined by posterior tooth and anterior truncate process; dactyl with denticulate proximal ridge, with smaller distal process bearing paired setae. Pereopod 3, coxa subrectangular, slightly larger than coxa 4, ventral margin rounded. Pereopod 4, anterior margin of coxa straight, posterior margin tapering. Pereopod 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, with 6–7 submarginal setae. Pereopod 7, coxa entire, submarginal setae lacking; basis spinose anteriorly, posterior margin expanded, with 6 serrations, each with a submarginal seta. Epimera typical. Uropods 1 and 2, outer rami shortened, spinose, approximately one-half length of inner. Uropod 3 missing. Telson broad, subrectangular, 1.3 times longer than wide, with 4 dorsofacial and 2 apical setae.

Leucomorphs. Unknown.

Etymology. Named for the type locality, Ningaloo Reef, Cape Range National Park, Western Australia.

Relationship. The more or less subequal coxae 2–4 and the thickened carpal lobe of gnathopod 2 of *A. ningaloo* are reminiscent of the *A. moana, A. kateluensis* and *A. bazimut* clade, but *A. ningaloo* lacks the apically notched inner plates of the maxilliped found in these central and south Pacific species.

Remarks. The single holotype specimen of *A. ningaloo* seems to show a slight apical indentation of the inner plate of the maxilliped that may represent incomplete fusion, natural malformation, or damage in dissection and mounting. Additional specimens must be examined before the value of this character is established.

Habitat. Presumed to be commensal, specific host(s) unknown, general habitat is shallow coral reef environments. It is worth noting here that this species was taken in an airlift sample from live coral (*Acropora*). Corals of the genus *Acropora* include 54 species from Western Australia. The complex branching growth pattern of *Acropora* provides a multitude of microhabitat and a number of commensals, including crustaceans, have been reported associated with *Acropora* corals. It is assumed that the habitat of *A. ningaloo* is the typical host ascidian or asconoid sponge. However, since *Acropora* inhabits shallow, wave washed reef flats, it

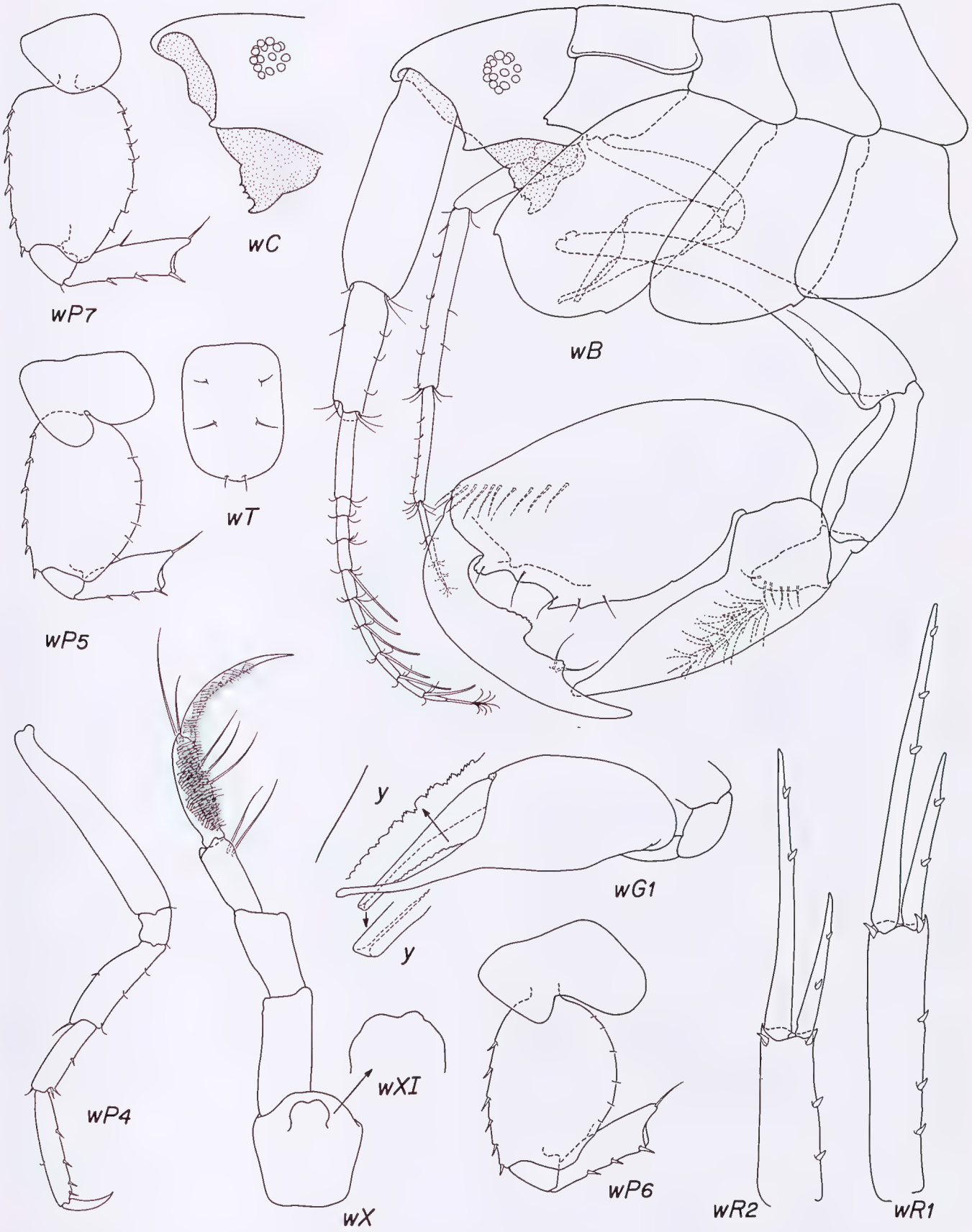

Fig. 14. *Anamixis ningaloo* n.sp., holotype, anamorph male "W", 2.63 mm.

is possible that anamorphs and leucomorphs of *A. ningaloo* could be found in secondary chambers, such as coral galls. The bases of *Acropora* colonies are frequently dead and overgrown with fouling communities that could support typical anamixid hosts. Further ecological studies are needed to resolve this issue.

Distribution. Eastern Indian Ocean, Western Australia, coral reefs, 2 m.

Anamixis pacifica (Barnard, 1955)

Fig. 10 (in part)

Leucothoides pacifica Barnard, 1955: 26–28, fig. 1a–k.
Anamixis linsleyi Barnard, 1955: 28–30, fig. 2a–d.

Material. Newport Beach, California; January, 1954; depth 15 m; J.L. Barnard and D.L. Reish.

Diagnosis. Propodus of gnathopod 1 with apical spine; palm of gnathopod 2 with several cusps, the distal one the longest.

Description. Head, anterior margin transverse, lower margin evenly rounded, ventral keel with low, sharp process. Antenna 1, ratio of articles 1–3, 14:10:7. Details of maxilliped unknown. Gnathopod 1, carpochelate, carpus recurved and blunt at apex; propodus with serrate inner edge and apical spine scarcely extending beyond carpus. Gnathopod 2, coxa ventrally expanded, lower margin demarcated by two small indentations; carpal lobe recurved, tapering; propodus, palm not distinct from hind margin, armed with several cusps, the distal one the longest; inner edge of dactyl with 3 cusps, the distal one armed with 2 spinules. Telson rounded apically, 1.5 times longer than wide, with several groups of marginal setae.

Leucomorphs. Unknown.

Relationship. *Anamixis pacifica* is unique in having a single terminal spine on the propodus of gnathopod 1. The second gnathopod appears intermediate in ornamentation between *A. cavatura* and *A. vanga* of the Caribbean.

Remarks. The anamorph was originally described as *A. linsleyi*. However, *A. pacifica*, initially described as *Leucothoides*, is assumed to be the leucomorph stage of *A. linsleyi* and takes page priority. This assumption is based on association of the two stages from the same localities and may prove problematic in the future if other anamixids are discovered from California waters. Until such time as confirmation can be obtained through rearing experiments, taxonomic decisions incorporating leucomorph characteristics of *A. pacifica* into *A. linsleyi* are to be avoided.

Habitat. From sponges found growing on floating docks.

Distribution. Eastern Pacific Ocean, Newport Bay, California, fouling communities.

Anamixis papuaensis n.sp.

Fig. 15

Type material. Anamorph male "A", 2.92 mm, AM P41032, *Galaxaura* algae from base of coral reef, east of Manunouha Island, Bootless Bay, Papua New Guinea, 9°30'S 147°07'E, 10 m, J.K. Lowry, 26 October 1980, station PNG-14.

Diagnosis. Head angle transverse. Ventral keel large, projecting will below head, bearing apically constricted tooth. Coxa 2 greatly enlarged; anterior margin expanded, with 4 small truncate cusps; ventral margin sinuous with midventral tooth. Gnathopod 2, carpus shortened, anterolateral margin serrate; propodus, hindmargin tapering, serrate, bearing a complex cuspate process on medial margin; distal portion with 2 large teeth; dactyl denticulate near insertion of propodus, distal margin with 2 blunt medial processes.

Description. Holotype "A". Head, anterior margin transverse, corner sharp; ventral keel enlarged, projecting will below ventral margin of head, bearing ventrally projecting tooth; eyes with 16 compact ommatidia. Lower lip lobes not readily visible from lateral view. Antennae: antenna 1, peduncle ratio 30:18:12; flagellum 10-articulate, aesthetascs on articles 8–9. Antenna 2, flagellum 4-articulate. Maxilliped, inner plates fused, small apical notch present; outer plates lacking inner lobes; palp article 4 elongate, 1.8 times length of article 3. Pereonite one with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 6 finely serrate on inner margin. Gnathopod 2, coxa greatly enlarged over coxae 3–4, anterior margin with 4 cusps, expanded, ventral margin sinuous with midventral tooth; medial margin of basis with distal triangular locking process; carpus short, anterolateral margin serrate; hindmargin of propodus tapering ventrally, serrate, mesoproximal region bearing large cuspate process; dactyl reaching to cuspate process of propodus, proximally denticulate, distomedial margin with blunt process, apex excavate. Pereopods 3 and 4, coxae subequal. Pereopod 5–6, coxae bilobed; second articles slightly rounded posteriorly. Pereopod 7, coxa entire, oval, article 2 similar to pereopod 5 and 6. Uropods 1 and 2, outer rami one-half length of inner. Uropod 3 missing. Telson broad, entire, 1.3 times longer than wide, bearing 2 small subapical setae.

Leucomorphs. Unknown.

Etymology. Named for the Papuan region of the South Pacific.

Relationship. *Anamixis papuaensis* appears most closely related to *A. falarikia* in the elongate palp

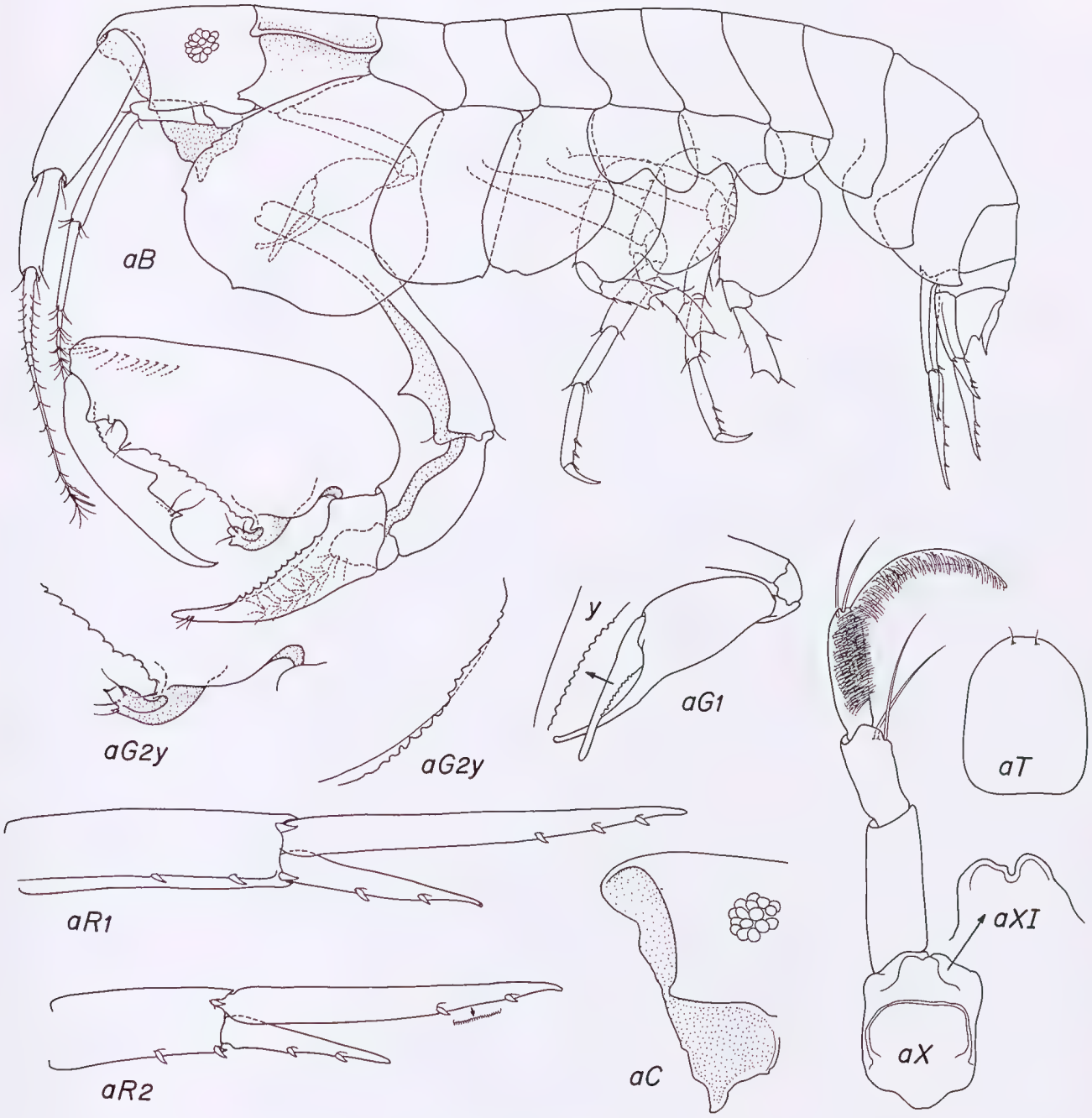

Fig. 15. *Anamixis papuaensis* n.sp., holotype, anamorph male "A", 2.92 mm.

article 4 of the maxilliped and features of the second gnathopod including an enlarged coxa with anterior cusps, a sinuous ventral margin with a midventral tooth, and an apically excavate dactyl. *Anamixis papuaensis* resembles *A. excalibur* in the elongate palp article 4 of the maxilliped.

Remarks. *Anamixis papuaensis* is clearly related to *A. falarikia* and *A. excalibur* by the elongate palp article 4 of the maxilliped. The similarities of *A. papuaensis* and *A. falarikia* including the morphology of coxa 2, the generally aberrant nature of the carpus, propodus, and dactyl of the second gnathopod indicate unusual variation along a common theme. The unique medial process on the inner margin of the second gnathopod of *A. papuaensis* may be an adaptation for a suspected commensal existence. *In-situ* behaviour studies of *A. papuaensis* and *A. falarikia* may elucidate the function of the atypical gnathopod 2 found in these two species.

Habitat. Unknown, suspected to be commensal in small asconoid sponges and ascidians.

Distribution. Coral Sea; south-eastern New Guinea, Papua New Guinea, coral reefs, 10 meters.

Anamixis stebbingi Walker, 1904

Anamixis stebbingi Walker, 1904: 259–261, fig. 18; ?Nayar, 1967: 44, fig. 6.

Diagnosis. Gnathopod 2, carpus denticulate near base, middistal portion with 2 raised processes.

Description. Gross morphology of most characters known only from original drawings, details on specific characters lacking in most instances.

Leucomorphs. Unknown.

Remarks. Walker's description of *A. stebbingi* from India was based on a single imperfect specimen, and only gnathopods 1 and 2 were partially figured. It now appears that there are several species from littoral coastal waters of India, all of which are closely related. All three species found in the region have the base of the carpal lobe on gnathopod 2 denticulate. *Anamixis barnardi, A. mahe* and *A. nedcampensis* exhibit a distinct thumb-like process on the carpus of gnathopod 2. Neither Walker's figure nor text description of gnathopod 2 mention such a process. Nayar (1967: 144, fig. 6) reported *A. stebbingi* from coastal India, his description also based on a damaged specimen. Nayar shows the carpus of gnathopod 2 with a small but distinct thumb-like process. However, he also shows a denticulate inner margin on the dactyl that is lacking in *A. barnardi*, but was figured by Walker in his description of *A. stebbingi*. Until additional material from the type localities are available for examination, *A. stebbingi* and *A. barnardi* will continue as distinct species, with Nayar's report of *A. stebbingi* problematical, falling intermediate between the two. It is probable that Nayar's material is an undescribed species. Considering distribution patterns in anamixids from other localities, it would not be unreasonable to expect another distinct species to occur in this region. Future species descriptions must include even the most minute details if subsequent authors are to sort out the species occurring within a given region.

Habitat. Oyster reefs.

Distribution. Indian Ocean, Sri Lanka (formerly Ceylon), sublittoral.

Anamixis tangaroa n.sp.

Fig. 16

Type material. HOLOTYPE, anamorph male "A", 3.58 mm, NMV 19742, Bass Strait, VIMS, cruise 81-T-1, NZOI RV *Tangaroa*, station 158, 13 November 1981, 39°49.5'S 146°18.5'E, 82 m, sediment: bryozoa mud, S-M grab. PARATYPES, anamorph males "B" 3.75 mm, and "C" 3.26 mm, NMV 19743, Bass Strait, Station 160, 13 November 1981, 39°43.7'S 147°19.6'E, 59 m, sediment: muddy shell, epibenthic sled.

Diagnosis. Inner plates of maxilliped, separate, incompletely fused; outer plates with vestigial inner lobes. Gnathopod 2, coxa ventrally excavate, inner margin of dactyl strongly tuberculate. Telson elongate.

Description. Holotype "A". Head, anterior margin transverse, anteroventral corner defined by small cusp; ventral keel truncate, barely extending below ventral margin of head, anterior margin oblique, straight, anterodistal region with several minute serrations; eyes with 14 compact ommatidia. Antennae, antenna 1, peduncular ratio 35:24:17, flagellum 12-articulate, aesthetascs on articles 10–12; antenna 2 approximately subequal to antenna 1, flagellum 4-articulate. Maxilliped, inner plates partially fused, outer plates with vestigial inner lobes; palp article 4, 1.2 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apex bifid; article 5 recurved apically, inner margin bare; article 6 straight, inner margin with minute, uneven serrations and setae, apex with accessory nail. Gnathopod 2, coxa somewhat larger than 2–4, anterior margin expanded smooth, ventral margin with broad excavation; carpus long, slightly recurved; propodus, hindmargin with several widely spaced setae, distal portion with 3 small teeth; dactyl, inner margin grossly tuberculate to paired setae. Pereopod 3, coxa smaller than 2 or 4, ventral margin rounded. Pereopod 4, coxa tapering posteriorly. Pereopods 5 and 6, coxae bilobed; basis spinose anteriorly, posterior margin expanded and furnished with 6–8 submarginal setae. Pereopod 7, coxa entire, posterior margin with 3 submarginal setae; basis spinose anteriorly, posterior margin with 14–15 submarginal setae. Uropods 1 and 2, peduncles and rami spinose, outer ramus one-half length of inner. Uropod 3 missing. Telson entire, elongate, 1.7 times longer than wide, with two pairs of dorsofacial, and one pair of apical setae.

Leucomorphs. Unknown.

Etymology. Named for the New Zealand Research Vessel, RV *Tangaroa*.

Relationship. The presence of incompletely fused inner plates on the maxilliped distinguish *A. tangaroa* from

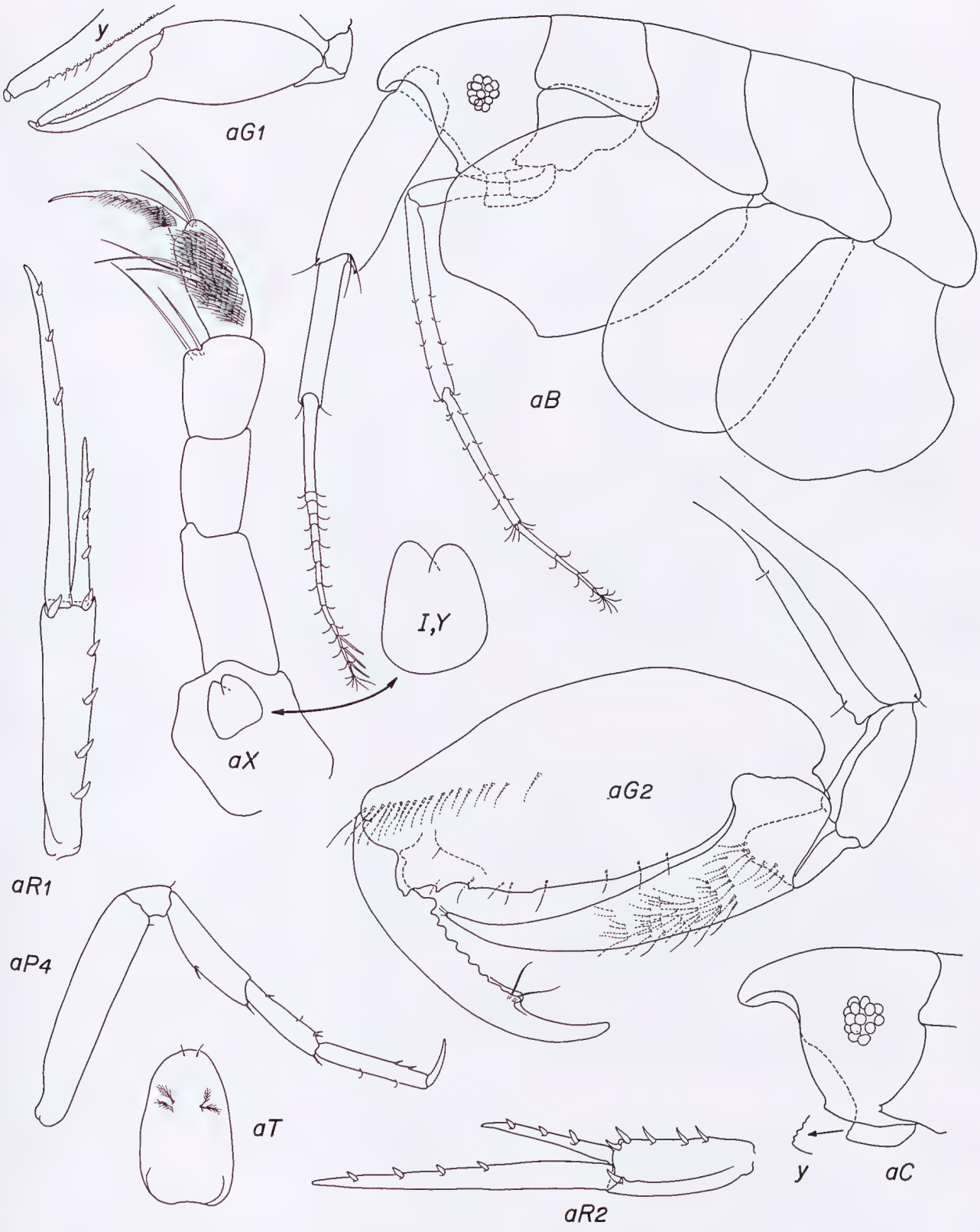

Fig. 16. *Anamixis tangaroa* n.sp., holotype, anamorph male "A", 3.58 mm.

all other members of the genus *Anamixis*, placing it in proximity with the genus *Nepanamixis* in this regard. The ventrally excavate second coxa and the strongly tuberculate inner margin of the dactyl of gnathopod 2 separate this species from other *Anamixis* species.

Remarks. The collection of *A. tangaroa* from depths over 80 meters in the cold waters of the Bass Strait (10°C) significantly extends the range of this typically tropical, shallow water family. *Anamixis tangaroa* may be a tropical relic (Newman, 1991) either from previous

sea level lowering, or, by prior tropical transgressions into lower latitudes. In either scenario, the plesiomorphic nature of *A. tangaroa* offers an interesting benchmark in the evolutionary history of the Anamixidae. The challenge will be to accurately integrate this information into the overall phylogeny of the group. On the other hand, it may that when we begin to adequately sample the deeper tropical waters, more of these unusual "relic" species will come to light.

Habitat. Presumed commensal, specific host(s) unknown.

Distribution. Tasman Sea, Bass Strait, coarse muddy sediments, 59–82 m.

Anamixis torrida Barnard, 1970

Anamixis torrida Barnard, 1970: 103, fig. 65a.
Leucothoides pottsi.–Schellenberg, 1938: 26–28, fig. 13.–J.L. Barnard, 1965: 492–493.–1970: 211–213, fig. 138 (not *A. pottsi* Shoemaker, 1933).–Ledoyer, 1984: 82 (as *L. torrida*).

Remarks. This species is based on a leucomorph and *A. torrida* should not be considered valid until it is connected with its anamorph counterpart. It is highly doubtful that the references to *A. torrida* by J.L. Barnard are valid and probably represent several species of possibly *Anamixis* and *Paranamixis*.

Anamixis vanga n.sp.

Figs 17,18

Type material. HOLOTYPE, anamorph male "E", 4.85 mm, USNM 243319, Carrie Bow Cay, Belize, rubble on reef slope, from the branchial basket of *Ascidia interrupta* Heller, 1878, 13.3 m, J.D. Thomas, 14 July 1988, JDT-Bel-132c; 1 PARATYPE, anamorph male "F", 4.34 mm, USNM 243320, JDT-Bel-132c; 3 PARATYPES, leucomorph male "G", 3.14 mm, USNM 243321, leucomorph female "H", 2.65 mm, USNM 243322, leucomorph female "I", 3.14 mm, USNM 243323, JDT-Bel-132c; 11 PARATYPES, 10 leucomorphs, 1 anamorph, USNM 243324, JDT-Bel-132c.

Additional material examined. USNM 243324, Carrie Bow Cay, Belize, rubble zone in backreef area north of Carrie Bow Cay, taken from the branchial basket of *A. interrupta*, located on the underside of coral rubble, 1 m, J.D. Thomas, 29 June 1987, JDT-Bel-112b; Carrie Bow Cay, Belize, rubble from patch reef near south-east corner of South Water Cut, 2 m, J. D. and S. Thomas, 24 July 1988, JDT-Bel-140.

Diagnosis. Anamorphs: head, lateral margins excavate, lacking any defining process; ventral keel subrectangular, scarcely projecting below head. Gnathopod 1, carpus and propodus each bearing a single terminal seta, inner margin of propodus dentate and setose. Gnathopod 2, propodus elongate, distal portion defined by 3 major teeth; dactyl without ornamentation. Leucomorphs: anterior margin of head broadly rounded; ventral keel projecting beneath head as a broadly rounded V-shaped process. Gnathopod 1, coxa subquadrate, bearing 2 apical setae; carpus, inner margin with minute serrations separated by larger serrate processes, apex with 2 embedded spines without ornamentation, the larger of the two with an accessory blade or flake; propodus, inner margin denticulate, armed with short spines and setae. Gnathopod 2, males, palm oblique, reaching Mark 0.65 on anterior margin of propodus.

Description. Based on holotype, male, "G", and paratype, male, "H". Head, lateral margin with prominent ridge, deeply excavate below, anterior margin oblique, lacking any defining processes; ventral keel projecting as a subrectangular process borne on posterior lamina; eyes composed of numerous ommatidia, bisected by lateral ridge. Antenna 1 elongate, ratio of segments 1–3 37:42:21; flagellum 12-articulate. Antenna 2 elongate, inserted well behind eye, flagellum 4-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.2 times the length of article 3. Pereonite 1 with prominent lateral locking ridge continuous with lateral ridge on head. Gnathopod 1, coxa with small apical process; carpus slightly recurved distally, inner margin unarmed, apex with long seta; propodus straight, not quite reaching the end of the carpus, inner margin denticulate, furnished with series of paired blunt spines and short setae, apex with long seta. Gnathopod 2, coxa much larger than 3 or 4, anterior margin with small cusp, ventral margin rounded, posterior margin straight, posteroventral corner with small cusp; carpus slightly recurved, bearing numerous mediofacial setal tufts; propodus long, hindmargin smooth, distal portion defined by a series of 3 teeth, the largest near insertion of dactyl, the remaining teeth becoming progressively smaller, inner surface with long row of mediofacial setae; dactyl nearly straight, bearing a seta on a small process. Pereopod 3, coxa slightly narrower than 2, rounded ventrally, posteroventral corner defined by small cusp. Pereopod 4, ventral margin of coxa emarginate posteriorly, posterior margin slightly expanded. Pereopods 5–6 similar, coxae bilobed, second articles with setose posterior lobe excavate ventrally. Pereopod 7, coxa entire, article 2 similar to pereopods 5 and 6. Epimera typical for family. Uropods 1 and 2, outer rami reduced. Uropod 3, outer ramus nearly as long as inner, spinose. Telson, suboval, 1.4 times longer than wide, bearing 2 small apical setae.

Description of leucomorphs. Based on male paratype "G", and female paratypes "H" and "I". Males similar to females in most aspects except for the relatively smaller second gnathopods and the presence of brood plates in females. Head, anterior margin broadly rounded,

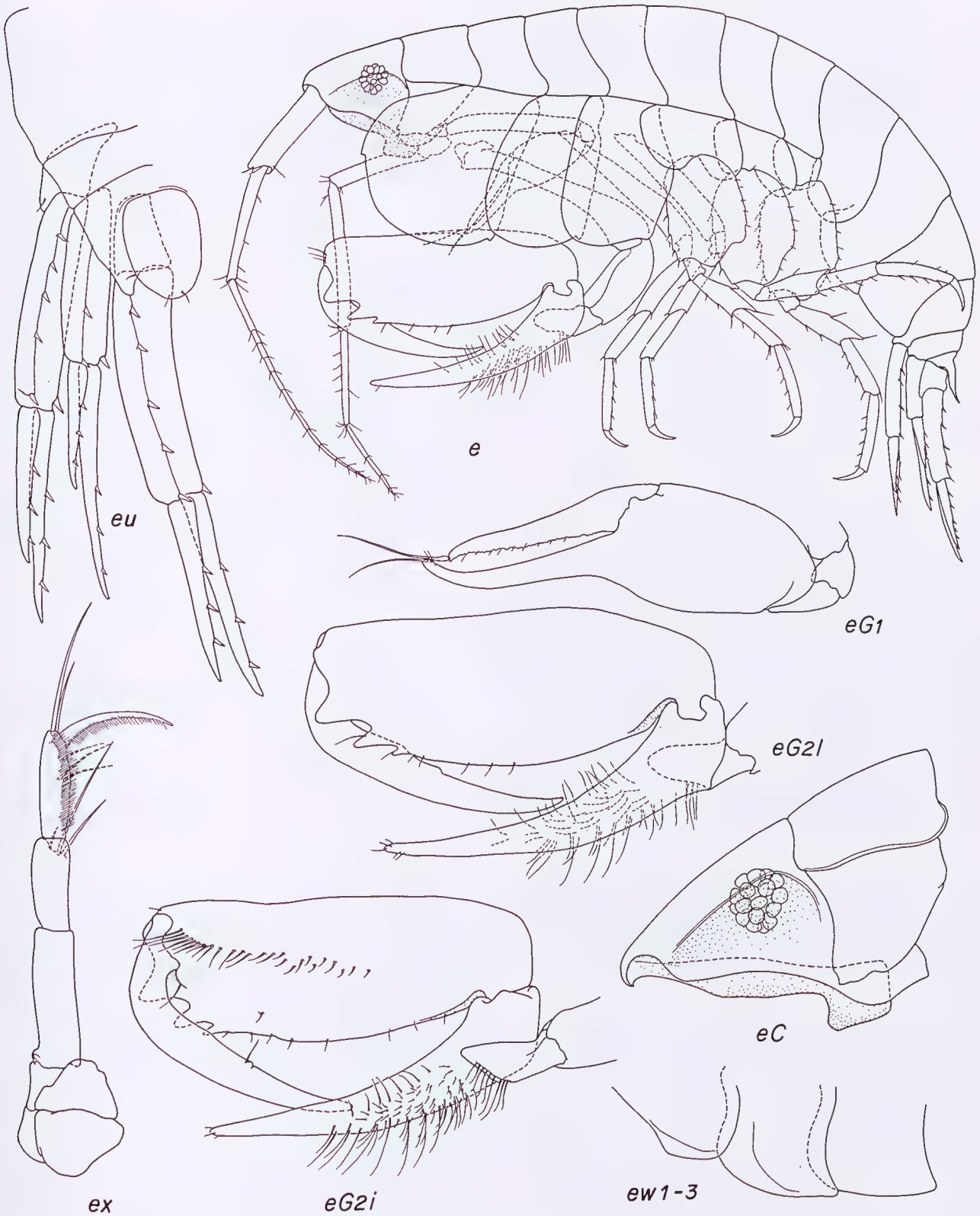

Fig. 17. *Anamixis vanga* n.sp., holotype, anamorph male "A", 4.85 mm.

lacking any defining processes; ventral keel oblique, subtruncate, anterior margin nearly vertical. Mouthparts normal for genus, left mandible with broad incisor and large lacinia mobilis; right mandible, incisor with hooked anterior margin, lacinia mobilis lacking. Gnathopod 1, coxa apically rounded with 2 closely spaced apical setae; carpus straight, inner margin finely serrate, with minute serrations separated by 9–12 elevated serrations, apex bearing 2 large spines embedded at Mark 0.77 of propodus, both spines lacking serrations, the larger spine with terminal flake; propodus, inner margin finely serrate, furnished with series of short

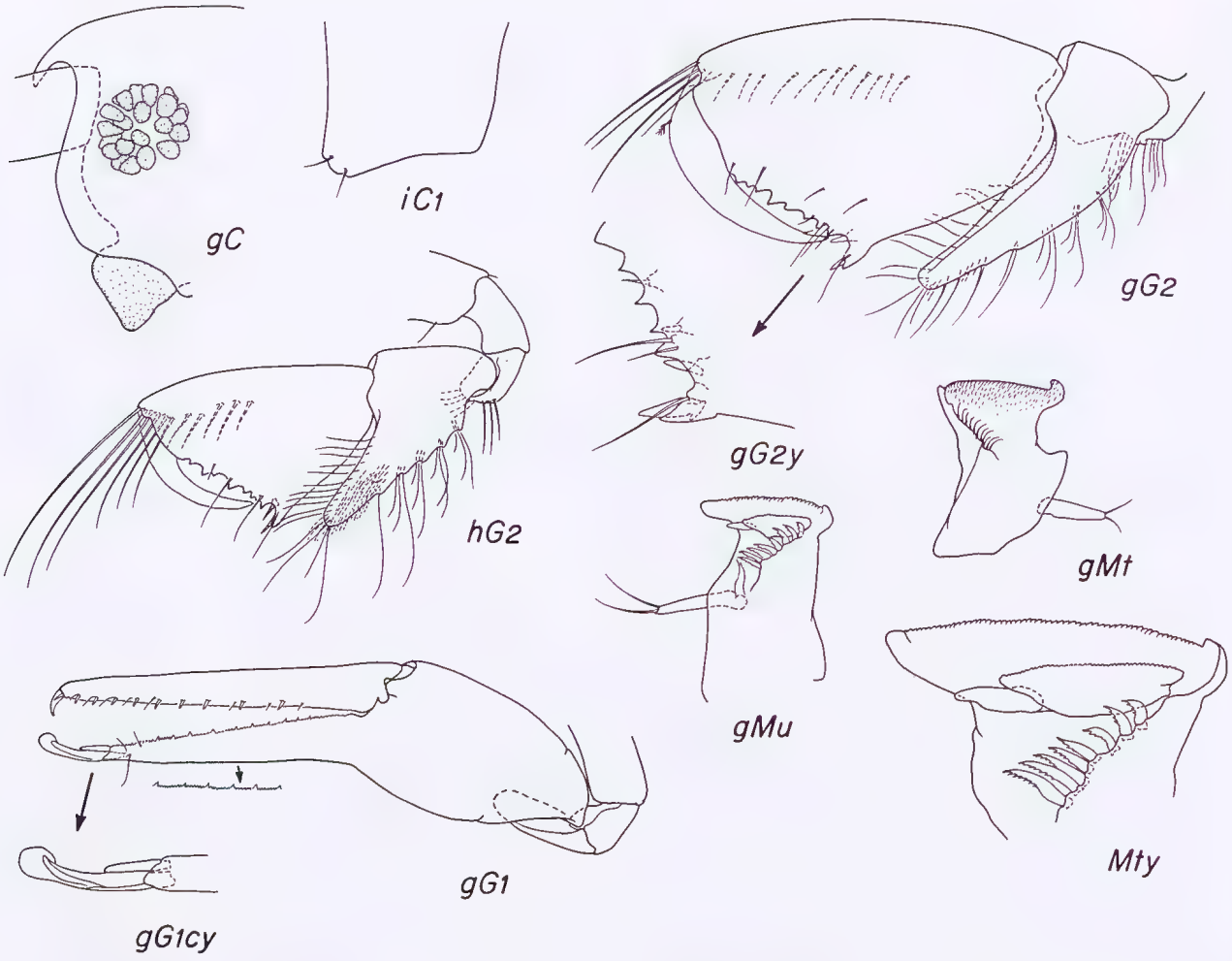

Fig. 18. *Anamixis vanga* n.sp., "G", leucomorph male, 3.14 mm; "H", leucomorph female, 2.65 mm; "I", leucomorph female, 3.14 mm.

spines and setae; dactyl represented with stout recurved spine. Gnathopod 2, in males, article 6 subquadrate, palm oblique, reaching Mark 0.65; in females, relatively smaller than males, article 6 subtriangular, palm oblique, reaching Mark 0.58, carpal setae numerous, and longer than in males.

Etymology. From the Latin, "vanga", meaning spade or mattock, referring to the appearance of the lateral margins of the head, noun in apposition.

Relationship. *Anamixis vanga* is readily separated from its nearest relative, *A. cavatura*, by the shape of the head and ventral keel, longer antennae; and the presence of 3 teeth on the propodus of gnathopod 2. Leucomorphs of these two species are separated on the basis of head margins, ventral keels, and general shape and armament of gnathopods 1 and 2.

Remarks. Colour in life and freshly preserved material: anamorphs, translucent pink, lacking any other significant coloration or patterns; leucomorphs, lacking any coloration and appearing transparent, internal organs readily visible through the exoskeleton.

All three Caribbean species of *Anamixis* have 2 long setae on gnathopod 1. The only other species of anamixid having long setae on gnathopod 1, *A. mahe*, from the Seychelles, differs in having an additional long seta on the propodus. The occurrence of this condition in such widely separated taxa could be attributed to convergence, possibly due to similar feeding adaptations or requirements. A similar argument could also be made for excavate lateral margins of the head exhibited by *A. vanga* and *Paranamixis kanu* from Papua New Guinea. Because anamixids are known or assumed commensals, the occurrence of convergent characters is not unusual. Such convergent morphologies can prove especially dangerous to the unwary taxonomist using cladistic methodologies. Great care must be taken to analyse and develop transformations series that incorporate those characters that will ultimately prove most informative in such analyses. The limited number of representative collections of amphipods from a wide variety of localities and the resulting inability to resolve details of specific character morphologies continue to be a hindrance in this regard.

Habitat. *Anamixis vanga* is most frequently collected from large, solitary tunicates in shallow coral reef or hard bottom areas. While occasionally taken from small asconoid sponges, the preferred host appears to be *Ascidia interrupta* Heller, 1878. The author has collected up to 4 anamorphs and 23 leucomorphs from the branchial basket of a single specimen of *A. interrupta*. Observations of *A. vanga* feeding within the host show that during feeding, *A. vanga* lowers the head ventrally, the lateral ridge on the head contacting the anterior margin of the large second coxa. The lateral ridge of the head thus may be used to "lock" the head in this position during feeding. The author speculates that this morphology may represent an adaptation found in species inhabiting larger hosts such as *A. interrupta* where the amphipods are subject to the relatively stronger current flow. For those species living in relatively smaller hosts, the locking ridge on the first pereonite appears sufficient to stabilise the head during feeding.

Distribution. Western Atlantic and Caribbean, from off Georgia to the Florida Keys, Belize; 2–20 m.

Anamixis yarrega (Barnard, 1974)

Leucothoides yarrega J.L. Barnard, 1974: 103; 1979: 130.
Anamixis yarrega.–Moore, 1987: 240–245, figs 1–4.

Diagnosis. Chelae of gnathopod 1 straight; dactyl of gnathopod 2 tuberculate on inner margin; coxa 4 concave posterodistally.

Description. Head, anterior margin transverse, defined by small cusp, eyes consisting of about a dozen scattered facets, ventral keel subrectangular, small. Antennae subequal in length. Antenna 1, ratio of articles 1–3 unknown, accessory flagellum minute, armed with 3 setae, flagellum 10-articulate. Antenna 2, slender, article 4 longer than 5; flagellum shorter than article 5, 4-articulate. Maxilliped, palp article 4, 1.30 times longer than article 3. Gnathopod 1, basis very elongate; carpus distally blunt, slightly upturned, with small terminal spine; propodus not quite reaching end of carpus, inner margin armed with short setae. Gnathopod 2, coxa large, margins smooth, 4 setae on anterior margin; carpus produced for 80 per cent of propodus length; propodus, hindmargin slightly expanded, merging into palm which is armed with several cusps, of which the anterior is the largest; dactyl straight to paired setae, then recurved, proximal margin denticulate. Uropods 1 and 2, outer ramus reduced to half the length of inner; uropod 3 missing. Telson suboval, entire, 1.38 times longer than wide. For a more detailed discussion of this species, see Moore (1987).

Leucomorphs. Unknown.

Remarks. Colour in life orange, with red eyes. This species is difficult to separate from other taxa as it possesses no striking characteristics. The ventral keel, of potential informative value, is unobservable in the holotype due to artefacts in the permanent slide preparation. Superficially, this species resembles *A. moana* but is distinguished by the subrectangular keel, the straight chelae on gnathopod 1, and the recurved carpal lobe and tuberculate inner margin of the dactyl on gnathopod 2. Moore's designation of a leucomorph for this species is premature and circumstantial.

Habitat. *Ecklonia radiata* and *Caulerpa trifaria* holdfasts.

Distribution. Tasman Sea, Tinderbox, Tasmania, 3–4 m.

Nepanamixis n.gen.

Type species. *Nepanamixis dianthus* n.sp.

Diagnosis. Terminal males: antennae relatively short, eyes with 9 scattered ommatidia, head margins rounded. Maxilliped, inner plates only partially fused, outer plates with inner lobes present or reduced to a small process. Coxa 1 moderately reduced. Gnathopod 1, carpus basally inflated, inner margin cuspate; when armed, apex of propodus with terminal spine or bulbous process. Coxae 2 dominant or subequal to 3 and 4; margins of coxae 2–3 smooth, sparsely setose submarginally; ventral margin of coxae 4 distally produced or crenulate. Gnathopod 2, propodus with 2 rows of mediofacial setae, each row with 4 or more seta, hindmargin straight or sinuous. Coxa 4 ventrally crenulate or excavate. Telson long, 1.80–2.10 or longer than wide, tapering apically.

Variables. Shape and armament of gnathopod 1 carpus and propodus; occurrence of tuberculations on anterior margin of the basis of gnathopod 2; extent of serrate lateral ridge on carpus of gnathopod 2; ventral margin of coxa 4.

Relationship. Differing from *Anamixis* and *Paranamixis* with the characters of the genus. Leucomorphs of *Nepanamixis dianthus* are unique in having a shortened carpus with 4 successively shortened, recurved spines on gnathopod 1; in having a more oblique palm in gnathopod 2. Leucomorphs currently known only from the type species of the genus, characters of other *Nepanamixis* species unknown at present.

Species. *Nepanamixis dianthus* n.sp.; *N. grossimana* (Ledoyer, 1978) as *Anamixis grossimana*; *N. torreanus* n.sp.; and *N. vectoris* n.sp.

Distribution. Marine, Indo-Pacific, Eastern Pacific, Western Caribbean, Mauritius to Belize, coral reefs, 1–10 m, 4 species.

Key to the Species of *Nepanamixis*

1. Gnathopod 2 of thick form, length 2.1–2.3 times width; apex of article 6, gnathopod 1 with bulbous process 3

—— Gnathopod 2 of thin form, length 2.8–3.0 times width; apex of article 6, gnathopod 1 lacking bulbous process 2

2. Gnathopod 1, apex of articles 5 and 6 with embedded spines, palm with 1 prominent tooth ..... *N. grossimana*

—— Gnathopod 1, apex of articles 5 and 6 lacking spines, palm with 2 prominent teeth ..... *N. dianthus* n.sp.

3. Article 5 of gnathopod 1 with stout spine at apex; coxa 4 emarginate ventrally ..... *N. vectoris* n.sp.

—— Article 5 of gnathopod 1 with small seta at apex; coxa 4 crenulate ventrally ..... *N. torreanus* n.sp.

Nepanamixis dianthus n.sp.

Figs 19,20

Type material. HOLOTYPE, anamorph male "A", 2.44 mm, USNM 243334, "Sand bores", Carrie Bow Cay, Belize, formalin wash of shallow rubble, 1–2 m, J.D. Thomas, 21 July 1984, JDT-Bel-105a. 1 PARATYPE, anamorph male "B", 2.39 mm, USNM 243335, Carrie Bow Cay, Belize, formalin wash of rubble in patch reef, south-west of reef crest on south side of South Water Cut, 1–2 m, J.D. Thomas, 5 July 1984, JDT-Bel-117; 1 PARATYPE, leucomorph male "C", 2.52 mm, USNM 243336, Carrie Bow Cay, Belize, formalin wash of *A. palmata* rubble, patch reef inside reef crest on South Water Cut, 1–2 m, J. D. Thomas, 9 June 1987, JDT-Bel-121a; 1 PARATYPE, leucomorph male "D", 2.00 mm, USNM 243337, JDT-Bel-121a; 1 PARATYPE, female leucomorph "E", 1.93 mm, USNM 243338, JDT-Bel 121a.

Additional material examined. Leucomorph, male, "F", 2.18 mm, (uncatalogued), Sand Bores, Carrie Bow Cay, Belize, formalin wash of rubble, 1–2 m, J.D. Thomas, 14 July 1988, JDT-Bel-133c.

Diagnosis. Gnathopod 1, carpus dilated, inner margin with 2 major and several minor cusps. Gnathopod 2, carpal lobe with prominent serrate lateral ridge, apex tapering; propodus elongate, 1.25 times longer than wide. Pereopod 4, coxa ventrally crenulate.

Description. Based on anamorph male: head, lateral margins rounded, anteroventral margin without defining cusps or processes, eye composed of 9 loosely scattered ommatidia; ventral keel projecting below margin of head, truncate. Antennae reduced in length; antenna 1 and 2, 0.61 and 0.59 the length of head to pereonite 4 respectively; antenna 1, ratio of articles 1–3 12:11:8, flagellum 4-articulate, of antenna 2, 3-articulate. Maxilliped, inner plates present, cleft; outer plates with distinct inner lobes; palp article 4, 1.1 times longer than article 3. Lower lip lobes not readily visible from lateral view. Pereonite 1, locking ridge present, scarcely produced posteriorly. Gnathopod 1, coxa reaching ventral margin of head, broadly rounded anteriorly; carpus, posterior margin inflated, inner surface with 2 prominent lateral cusps and 4 minor processes medially; propodus straight, inner margin with setae only, apex lacking ornamentation. Gnathopod 2, coxa larger than 3 or 4, margins smooth, broadly rounded with 3 ventral setae; basis unarmed; carpal lobe with pronounced serrate lateral ridge flared outwards, distal portion of carpus attenuate, apex with several small setae; propodus elongate, 3.12 times longer than wide, hindmargin sinuous, apex truncate and lacking defining ornamentation, secondary row of 5 mediofacial setae present; dactyl elongate, recurved distally, with 2 small paired setae, tip of dactyl nearly reaching entire length of palm. Pereopod 3, coxa smaller than 4, margins not expanded, with 2 ventral setae; remainder of pereopod normal. Pereopod 4, coxa 4 crenulate ventrally, with 3 setae; remainder of pereopod similar to pereopod 3. Pereopods 5 and 6 similar except for deeper hind lobe on coxa 6; bases spinose anteriorly, posterior margins uneven, tapering ventrally and setose. Pereopod 7, coxae entire, basis slightly more expanded than 5 or 6, otherwise similar to 5 and 6. Epimera normal for genus. Uropods 1 and 2, outer rami reduced, outer ramus of uropod 1 lacking spines and styliform. Uropod 3, outer ramus nearly subequal to inner. Telson, elongate, subovate, 1.87 times longer than wide, apex evenly tapered and bearing 2 setae.

Leucomorphs. Confirmed from rearing experiments. However, selected leucomorph males apparently undergo a terminal transformation, persisting as leucomorphs

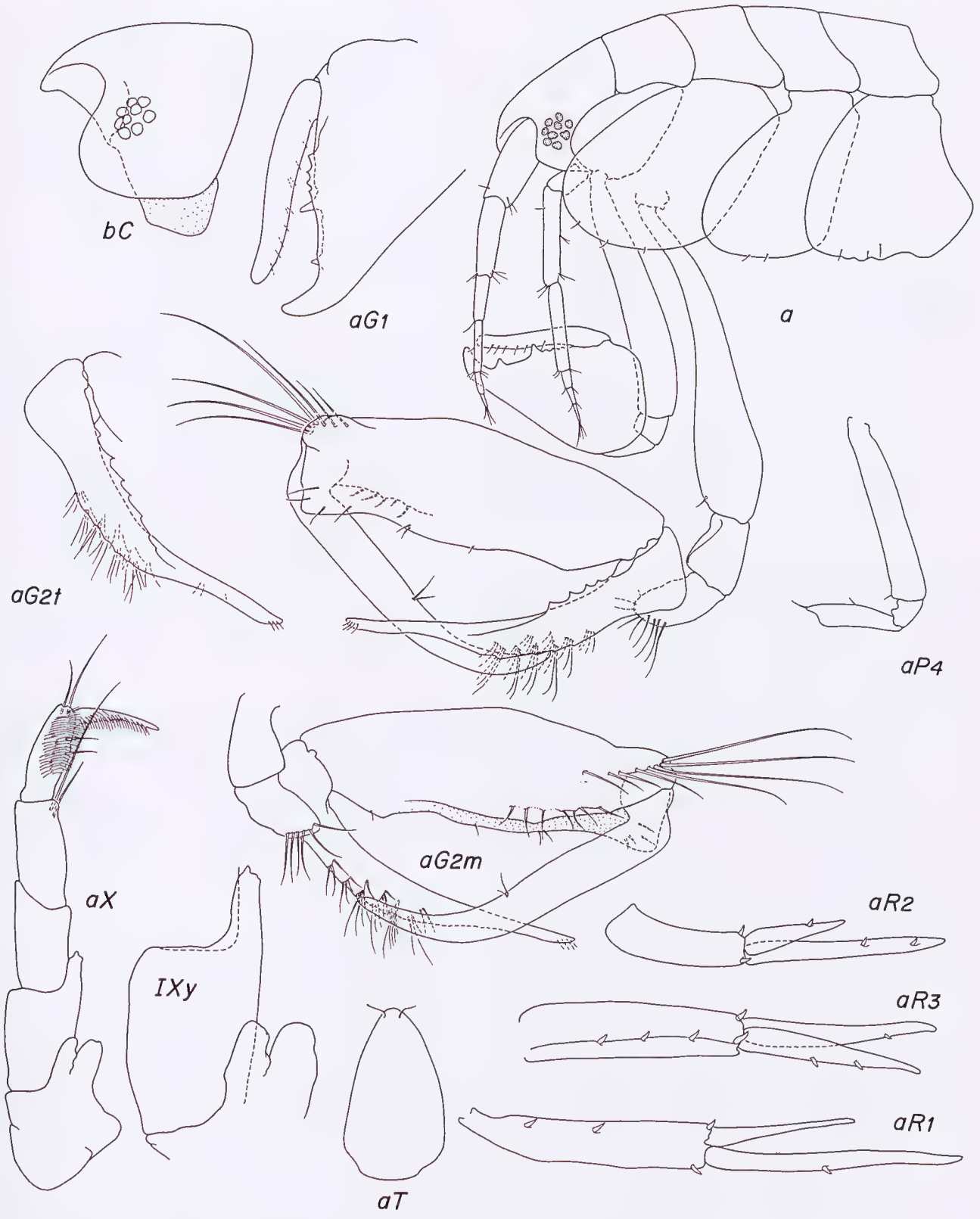

Fig. 19. *Nepanamixis dianthus* n.sp., holotype, anamorph male "A", 2.44 mm; "B", anamorph male, "B", 2.39 mm.

that are larger in size than their anamorph counterparts. Such males are characterised by large second gnathopod with a more oblique palm than smaller male leucomorphs (see leucomorph male "C").

Description of sub-adult male and female leucomorphs: head, anterior margins rounded, eye composed of 9 loosely packed ommatidia. Maxilliped, inner plates separate, apices with 3 marginal spines; outer plate

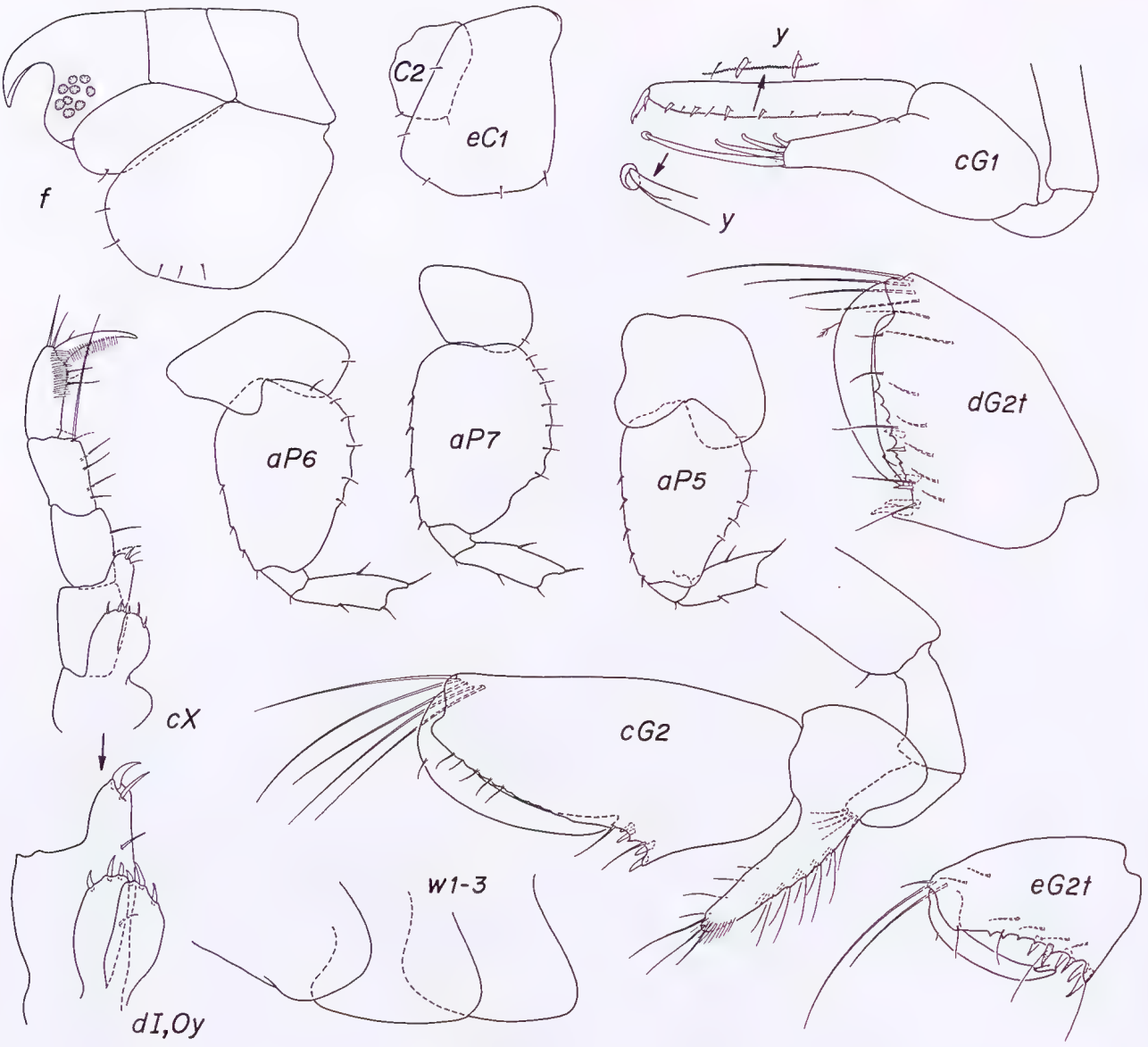

Fig. 20. *Nepanamixis dianthus* n.sp., holotype, anamorph male "a", 2.44 mm; "c", leucomorph male, 2.52 mm; "d", leucomorph male, 2.00 mm; "e", leucomorph female, 1.93 mm; "f", leucomroph male, 2.18 mm.

produced medially, apex with 1 large and 1 medium spine. Gnathopod 1, coxa reduced, rounded, extending below margin of head; carpus shortened, apex only reaching to midpoint of propodus, apex with 4 embedded spines, the largest reaching apex of propodus and bearing terminal flake, the three remaining spines successively shortened; propodus minutely serrate on inner margin with 4 equally spaced submarginal spines and setae, apex with stout spine. Gnathopod 2, coxa large, evenly rounded; carpus, palm multidentate, inner margin with 6 embedded spines, the largest defining the palm; palm oblique, inner margin with two rows of feeding setae; dactyl slightly recurved, reaching to second pair of embedded spines.

Sexual dimorphism. Non-transformed, non-terminal males and females are similar in all aspects except for the relatively smaller gnathopod 2 of females, the palm of which is more oblique than males and slightly excavate. Terminal male leucomorphs develop a greatly elongated carpus of gnathopod 2, the palm becoming even more oblique and bearing two groups of embedded spines near the palmar margin. Gnathopod 1 is essentially similar in all respects. It is currently not known whether this stage is a separate terminal leucomorph state, or, whether this stage, non-transformed males, or both, are capable of transforming into an anamorph stage. Because this hyper-developed male stage exists at a size larger than that recorded for some of the smaller anamorphs it may represent another terminal condition unique to this species. Leucomorph counterparts for other species of *Nepanamixis* are unknown, but their discovery could shed light on this interesting situation.

Relationships. *Nepanamixis dianthus* resembles *N. grossimana*, from the reefs of Mauritius, in the maxilliped,

the general shape of gnathopods 1 and 2. *Nepanamixis dianthus* differs from *N. grossimana* in the following characters: in having 2 major cusps in the inner margin of the propodus and in lacking an apical spine in both the carpus and propodus; in gnathopod 2 lacking the conspicuous serrate lateral carpal ridge and the sinuous margin of the palm; in uropod 1 with the outer ramus lacking spines (versus the inner ramus in *N. grossimana*); and in the apically pointed telson. Unfortunately, leucomorphs are undocumented for *N. grossimana*, but it is assumed that they would share similar qualities as those of *N. dianthus*. The unique juvenile morphology exhibited in *N. dianthus* provides strong evidence for the value of juvenile characters in helping to unravel the taxonomy of anamixids. Based on this evidence it can be postulated that the more plesiomorphic *Nepanamixis* is possibly an ancestral form from which both *Anamixis* and *Paranamixis* are derived. Additional specialised collecting efforts from reefs in Pacific Ocean and the Caribbean should reveal more representatives of *Nepanamixis* and provide additional information regarding the early evolution of this group.

Colour of anamorphs and leucomorphs in live and freshly preserved material is a translucent pink, fading rapidly in preservative to a nearly transparent condition.

Etymology. From the Latin "dianthus", meaning carnation pink, referring to the colour of live and freshly preserved specimens.

Habitat. Specific habitat unknown, all specimens have been taken from deep within coral rubble, assumed to be commensal, but it is possible that the unique morphologies in *N. dianthus* are adaptations to highly cryptic habitats are precursors to commensalism.

Distribution. Western Caribbean Sea; Belize, among coral rubble. 2–8 m.

Nepanamixis grossimana (Ledoyer, 1978)

Anamixis grossimana Ledoyer, 1978: 229, fig. 13(II).

Diagnosis. Gnathopod 1 with 1 major and 1 minor cusp on palm of carpus, carpus and propodus with apical spine; gnathopod 2, carpus serrate proximally, hind margin of propodus straight; bottom margin of coxa 4 with shallow emargination.

Description. Head, lateral margin rounded, ventral keel unknown. Antennae 1 and 2 subequal in length; antenna 1 with small, 1-articulate accessory flagellum; ratio of articles 1–3 of antenna 1, 7:10:5; flagella 7 and 4-articulate respectively. Maxilliped, inner plates consisting of 2 small lobes separated by evagination; outer plates with distinct inner lobes. Gnathopod 1, coxa half as deep as coxa 2, evenly rounded; basis thick, with 10–11 scattered tubercles along anterior margin; carpus with 1 major cusp and 9–10 small tubercles on palm, with thick apical spine; propodus, inner margin nodulose, apex with thick spine. Coxa 4 with slight ventral emargination. Bases of pereopods 5–7 narrow, hind margin of 7 with large serrations. Telson elongate, 1.88 times longer than wide, apically truncated, tridentate.

Relationship. *Nepanamixis grossimana* is most closely related to *N. dianthus* with which it shares several features: general shape of gnathopods 1 and 2; emarginate ventral margin of coxa 4; relatively narrower article 2 on pereopods 5–7; and an elongate telson. *Nepanamixis grossimana* differs from *N. dianthus* in small details of these same features: gnathopod 1, basis with small tubercles on anterior margin; in having only 1 major cusp on the palm; in having a nodulose inner margin on the propodus; and in having thick terminal spines on both carpus and propodus; in having the basis of gnathopod 2 with small anterior tubercles (not illustrated); in the carpal lobe having only the proximal portion scarcely denticulate; and in having a straight hind margin on the propodus.

Remarks. Ledoyer's original figures for *N. grossimana* clearly shows the distinct condition of the maxilliped that places this species in the genus *Nepanamixis*. Examination of the single type specimen in permanent slide mounts has revealed a number of characters not discussed or illustrated in the original description. Leucomorphs are unknown for this species, but examination of collections for leucomorphs similar to those of *N. dianthus* should reveal specimens with characters of the genus. *Nepanamixis dianthus* and *N. grossimana* are more closely related to each other than either is to the Eastern Pacific species *N. torreanus* and *N. vectoris*, indicating that *N. grossimana* and *N. dianthus* may have shared an ancestor with a wide geographical distribution and that the Eastern Pacific species may have arisen after the ancestral distribution experienced an isolating vicariant event. It is highly unlikely that these species came to exist in their present distributions by dispersal.

Habitat. Coral rubble, Balaclava Reef.

Distribution. Indian Ocean, Mauritius, coral reefs, especially shallow rubble areas.

Nepanamixis torreanus n.sp.

Fig. 21

Type material. HOLOTYPE, anamorph male "B", 2.52 mm, USNM 243340, Darwin Bay, Tower Island, Galapagos, shore collection of *Porites* at Seal Beach, 1 m, 22 February 1933, Alan Hancock Expedition, Station 94-33.

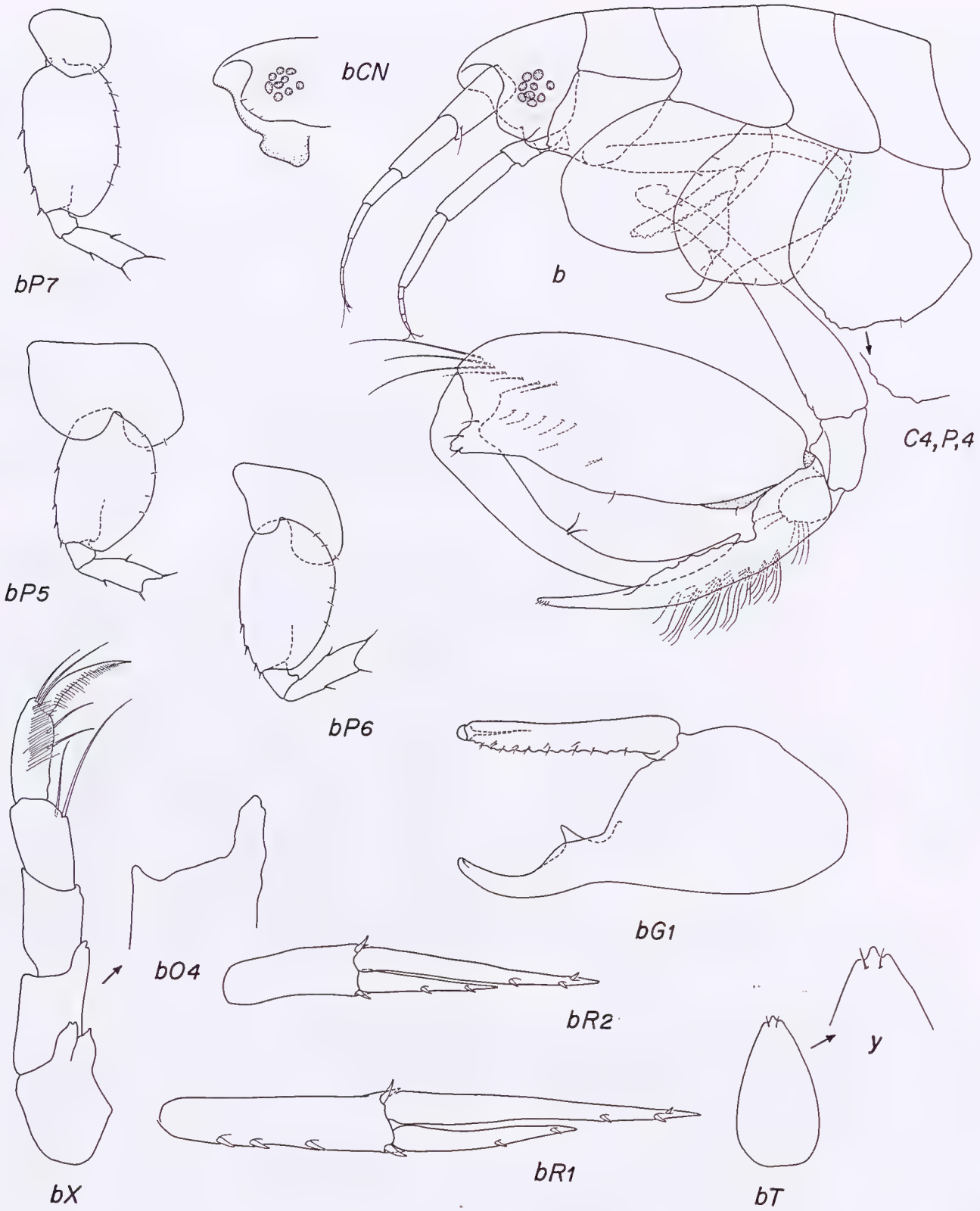

Fig. 21. *Nepanamixis torreanus* n.sp., holotype, anamorph male, "B", 2.52 mm.

Diagnosis. Coxa 4 crenulate ventrally; gnathopod 1, apex of carpus with minute setule; telson, with midapical projection.

Description. Head, lateral and ventral margins rounded; eyes composed of 9 diffuse ommatidia; ventral keel scarcely produced, rounded, subrectangular. Antenna 1 and 2, 0.60 and 0.53 the length of head to pereonite

4. Antenna 1, ratio of articles 1–3, 14:14:8; flagellum with 4 elongate articles. Antenna 2, flagellum composed of 4 shortened articles. Lower lip lobes visible in lateral and ventral view. Maxilliped, inner plates cleft, apices produced; outer plate prominent, apices produced, reaching 0.45 mark of palp article 1; palp article 4, 1.09 times as long as article 3. Pereonite 1 with small lateral locking ridge. Gnathopod 1, coxa reaching bottom margin of head, anteroventral apices bifid; carpus expanded basoproximally, inner margin bearing a large, sharp process, apex with small setae; propodus linear, inner margin with scattered tuberculations and setae, apex with fleshy bulbous process. Gnathopod 2, coxa subequal in size to 3 and 4, margins smooth, evenly rounded; carpus with proximolateral ridge scarcely serrate; propodus, hindmargin sinuous distally, posterodistal margin defined by large process, inner margin with secondary row of 5 mediofacial setae plus 2 additional isolated setae; dactyl elongate, recurved, nearly reaching to base of carpus, with 2 paired setae. Pereopod 3, coxa slightly smaller than coxa 2 or 4, ventral margins rounded, anterior and ventral margins with scattered submarginal setae, posteroventral corner with small cusp; remainder of pereopod normal. Pereopod 4, ventral margin of coxa produced and crenulate; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed, hind lobe equal to front; basis evenly rounded, posterior margin with scattered submarginal setulae. Pereopod 6, coxa bilobed, hind lobe larger and deeper than front lobe; basis evenly rounded. Pereopod 7, coxa small, entire, with 2 posteroventral setae; basis somewhat deeper than 5 or 6, hind margin dentate and setose. Epimera normal for genus. Outer ramus of uropods 1 and 2 reduced. Uropod 3 missing. Telson suboval, 1.82 times longer than wide, tapering distally, apical margin produced into a triangular projection with 2 subapical setae.

Leucomorphs. Unknown.

Etymology. From the Spanish "torreanus" meaning tower, referring to the type locality, Tower Island, Galapagos.

Remarks. *Nepanamixis torreanus* bears a strong superficial resemblance to *N. vectoris* but differs in the more deeply cleft inner plates and larger inner lobes of the outer plates of the maxilliped; in the apically bifid coxa and lack of a large embedded spine in the apex of the carpus of gnathopod 1; in the less pronounced serrations on the carpal lobe of gnathopod 2; the ventrally crenulate coxa 4, and the apical process on the telson. The fact that *N. torreanus* retains the plesiomorphic condition of the inner and outer plates of the maxilliped, while *N. vectoris* retains only the slightest remnant of this structure, supports the hypothesis that taxa from remote island archipelagos tend to retain plesiomorphic characters, while related taxa from continentally associated habitats tend to exhibit apomorphic trends in certain morphologies. While *N. grossimana, N. torreanus* and *N. dianthus* all retain, to some degree, the inner lobes of the outer plates of the maxilliped, the similarity of other characters between *N. grossimana* and *N. dianthus* argues for a closer relationship between these two species than either is to *N. torreanus* or *N. vectoris*.

Habitat. Unknown, assumed to be commensal.

Distribution. Pacific Ocean; Tower Island, Galapagos, among coral rubble, 1 m.

Nepanamixis vectoris n.sp.

Fig. 22

Type material. HOLOTYPE, anamorph male "A", 2.69 mm, USNM 131571, Pinas Bay, Panama, coral in South Bay, mainland side, 2–4 fathoms, Alan Hancock Expedition, 29 January 1935, Hancock-444-35.

Diagnosis. Anterior margin of basis of gnathopod 1 and 2 weakly tuberculate. Gnathopod 2, carpal process with elevated serrate ridge on lateral margin extending proximally to insertion of propodus. Gnathopod 1, carpus with large apical spine; propodus, apex with blunt, bulbous process.

Description. Head, rounded laterally, ventral margin evenly rounded with 4 submarginal setulae, eye composed of 9 slightly dispersed ommatidia, ventral keel scarcely extending below head, posterior portion subrectangular. Antenna 1 missing beyond peduncle segment 1. Antenna 2, 0.55 the length of head and first four pereonite segments; flagellum 4-articulate. Lower lip lobes visible from lateral and ventral view as 2 small fleshy processes. Maxilliped, inner plates partially fused, apically cleft one-third of length; outer plates with vestigial inner lobes, represented by minute process on inner margin; palp article 4, 1.23 times longer than article 3. Pereonite 1 with lateral locking ridge, not produced posteriorly. Gnathopod 1, coxa reduced, extending to ventral margin of head or below; anterior margin of basis weakly tuberculate; proximal portion of carpus expanded, inner margin with single large cusp, apex with large embedded spine; article 6 straight, reaching end of article 5, inner margin nodulose, apex with bulbous process. Gnathopod 2, coxa slightly larger than 3 or 4, margins smooth; basis dilated distally, anteroproximal margin with several small tubercules (not illustrated); carpus, elevated serrate lateral ridge extending to basal portion of carpal margin, apex with 4 setae; propodus with secondary row of 5 setae; ventral margin defined by a single large serrate process, hindmargin smooth; dactyl long, recurved, with 2 setae on inner margin. Pereopod 3, coxa smaller than 2 or 4, evenly rounded ventrally. Pereopod 4, coxa with

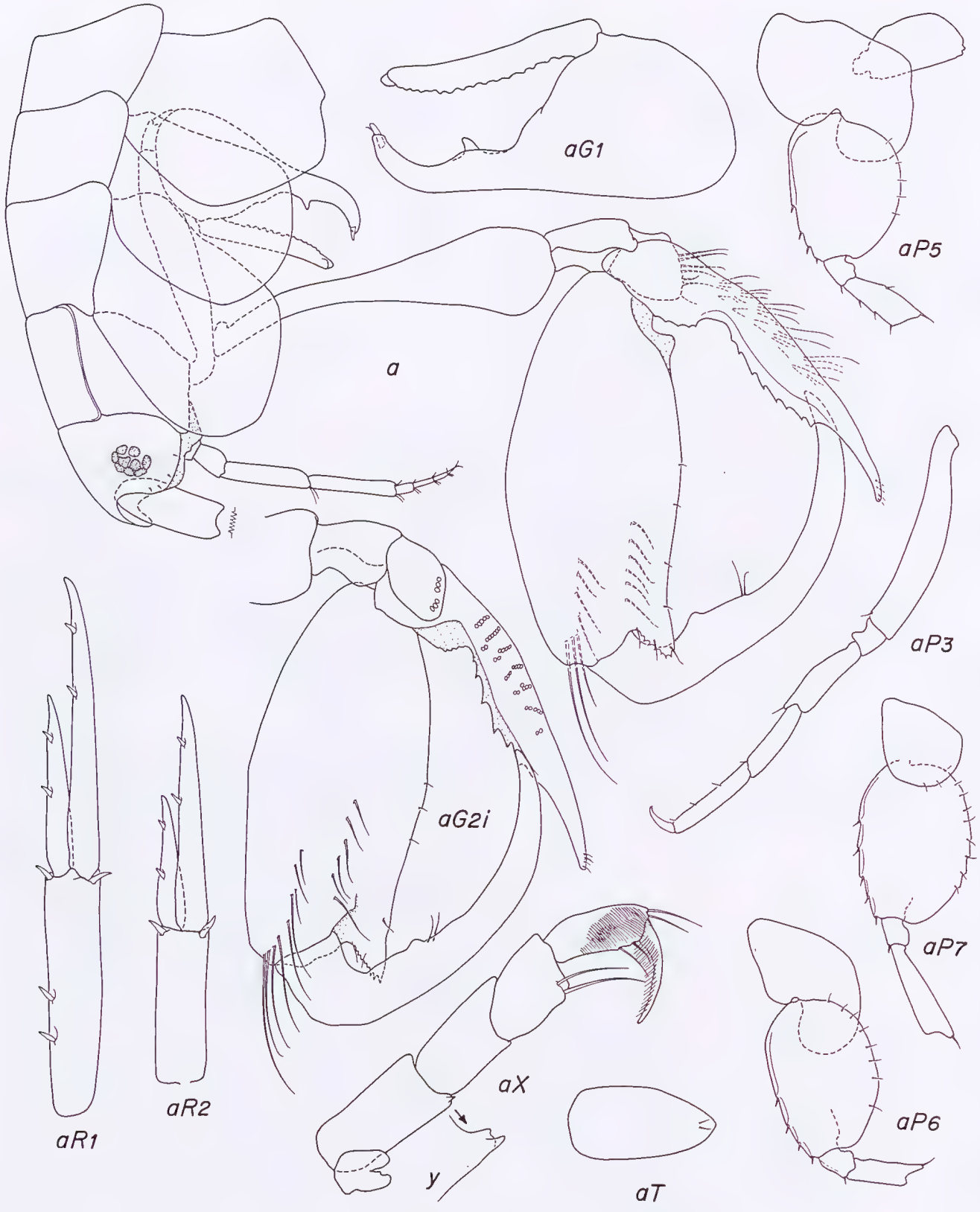

Fig. 22. *Nepanamixis vectoris* n.sp., holotype, anamorph male "A", 2.69 mm.

anterior, ventral and posterior margins produced, posterior portion of ventral margin tapering, with small cusp in midventral region, posterior margin slightly excavate. Pereopod 5, coxa bilobed, hind margin not produced; basis, posterior margin evenly expanded. Pereopod 6, hind margin of coxa produced ventrally; basis similar to pereopod 5. Pereopod 7, coxa entire, with 2 setae along posteroventral margin; basis expanded, small

indentations with small setae. Epimera normal. Uropods 1 and 2, outer ramus reduced; uropod 3 missing. Telson elongate, 2.08 times as long as wide, apex produced, 2 subapical setae.

Leucomorphs. Unknown.

Etymology. From the Latin "vecta" meaning passenger, referring to the commensal habits of anamixids.

Remarks. *Anamixis vectoris* shares a superficial resemblance to *A. torreanus* in the eyes, head margins, and gnathopods 1 and 2. *Anamixis vectoris* differs from *A. torreanus* in the following characters: outer plates of maxilliped with vestigial inner lobes; gnathopod 1, coxa apically rounded, basis with small tubercles along anterior margin; carpus with apical spine. Gnathopod 2, basis with small tubercles along anterior margin; carpus with more pronounced lateral serrations; propodus, large defining cusp serrate. Coxa 4, ventral margin with single cuspate process, lacking the crenulations of *A. torreanus*.

Habitat. Unknown, assumed to be commensal.

Distribution. Eastern Pacific Ocean, Panama, from coral reefs, 4–8 m.

Paranamixis Schellenberg

Paranamixis Schellenberg, 1938: 29.

Type species. *Paranamixis bocki* (Schellenberg, 1938), monotypy.

Diagnosis. In terminal males: antennae relatively long. Inner plates of maxilliped partially or completely fused, apically cleft or entire; outer plates lacking inner lobes. Coxa 1 greatly reduced, remainder of gnathopod 1 absent in post-transformational moults, occasionally represented by small vestige in transformational males. Article 2 of gnathopod 2 normally smooth, occasionally with serrate anteroproximal ridge. Telson 1.2–1.5 times longer than wide.

Relationship. Differing from *Anamixis* in lacking gnathopod 1 in post-transformational moults. Differing from *Nepanamixis* in the relatively longer antennae; more numerous ommatidia; in lacking inner lobes on the outer plates of the maxilliped; the lack of gnathopod 1; in having a single row of mediofacial feeding setae on the propodus of gnathopod 2; in having a ventrally rounded coxa 4; and in the relatively shorter telson.

Remarks. Leucomorphs are undocumented for any species in this genus. Detailed analyses are needed on the maxillipeds of all *Paranamixis* to determine the condition of the inner plates. Until such information is available, the genus is retained.

Species. *Paranamixis aberro* Hirayama, 1983; *P. bocki* Schellenberg, 1938; (?Ruffo, 1969; Ledoyer, 1978); *P. clarkae* n.sp.; *P. denticulus* Kim & Kim, 1991; *P. excavatus* Ledoyer, 1978; *P. fijiensis* n.sp.; *P. indicus* Sivaprakasam, 1968; (?Ledoyer, 1979); *P. kanu* n.sp.; *P. madagascarensis* Ledoyer, 1982; (?Myers, 1985 = *P. fijiensis*); *P. misakiensis* n.sp.

Distribution. Marine, Polynesia to Madagascar, coral reefs, 0–4 m, eight species.

Key to the Species of *Paranamixis*

1. Coxa 2, anterodistal margin with midventral projection(s), cusp(s), or serrations 8
—— Coxa 2, anterodistal distal margin evenly rounded 2
2. Coxa 2, anteroproximal margin evenly rounded 3
—— Coxa 2, anteroproximal margin expanded ..... *P. fijiensis* n.sp.
3. Head, anterior margin transverse or slightly produced, ventral margin horizontal, anteroventral corner defined by small upturned cusp 4
—— Head, anterior margin oblique, ventral margin lacking or oblique, anteroventral corner lacking upturned cusp 5
4. Anterior margin of head slightly produced; coxa 2, anterior margin smooth; uropods spinose ..... *P. madagascarensis*
—— Anterior margin of head transverse; coxa 2, anterior margin with 2 cusps; uropods without spines ..... *P. indicus*

5. Head, ventral oblique margin with mid lateral notch, lateral margins rounded 6

—— Head, ventral oblique margin continuous, lacking any defining notch or cusp, lateral margins with elevated ridge, head excavate below ..... *P. kanu* n.sp.

6. Gnathopod 2, anterior margin of coxa rounded, basis with serrate distomedial locking ridge, anterior margin of carpus minutely toothed, hindmargin of propodus finely serrate, inner margin of dactyl tuberculate 7

—— Gnathopod 2, anterior margin of coxa expanded forward, basis with triangular anteromedial locking ridge; anterior margin of carpus smooth, hindmargin of propodus smooth with scattered setae; inner margin of dactyl smooth ..... *P. aberro*

7. Gnathopod 2, coxa with anteroventral and posteroventral cusps, anterior margin of carpus toothed, inner margin of dactyl with 8–9 continuous tubercles ..... *P. misakiensis* n.sp.

—— Gnathopod 2, anterior margin of coxa smooth, inner margin of dactyl with 4–5 disjunct tubercles ..... *P. denticulus*

8. Eyes, ommatidia diffuse; anterodistal margin of coxa 2 with serrate process ..... *P. excavatus*

—— Eyes, ommatidia compact; anterodistal margin of coxa 2 lacking serrate process 9

9. Gnathopod 2, anterodistal margin of coxa rounded, ventral margin with sharp process; anteroproximal margin of article 2 of gnathopod 2 finely serrate; article 2 of pereopod 5 subquadrate on posterior margin ..... *P. bocki*

—— Gnathopod 2, anterodistal margin of coxa slightly excavate, ventral margin with a small, produced point; anteroproximal margin of article 2 of gnathopod 2 grossly serrate ..... *P. clarkae* n.sp.

Paranamixis aberro (Hirayama, 1983)

Paranamixis aberro Hirayama, 1983: 143–146, figs 36,37.

Diagnosis. Head margin oblique with distinct concavity near midsection; coxa 2, anterior margin expanded forward to middle of head, margins smooth; gnathopod 2, basis with thin triangular protrusion on anteromedial margin, posterodistal portion of propodus excavate, bearing 3 teeth.

Description. Ventral keel subtriangular, projecting beneath head, directed slightly anteriorly. Antennae subequal in length, shorter than half as long as body. Antenna 1, ratio of articles 1–3, 20:10:5; peduncular segment 1 stout, with several small setae, article 2 much thinner than 1, with many setae; accessory flagellum small, uniarticulate with apical pair of setae; flagellum 9-articulate. Antenna 2, flagellum 4-articulate. Gnathopod 2, coxa larger than 3 or 4, expanded forward, rounded, smooth marginally, lower margin setose; basis with thin triangular protrusion on anteromedial margin; carpus recurved; propodus, posterodistal margin with 3 teeth, gradually increasing in size distally; dactyl with pair of setae at distal third of article. Coxa 6, posterior lobe about twice the anterior lobe in width and depth. Telson broad, entire, 1.55 times longer than wide, distal margin rounded, with 2 minute setae, dorsal margin with two opposite rows of 2 single setae and 2 paired setae, all setae pinnate.

Leucomorphs. Unknown.

Relationship. *Paranamixis aberro* is separated from other *Paranamixis* species by the unique configuration of the head margin, otherwise it exhibits no clearly distinct group of characteristics.

Remarks. Hirayama's description and figures of *P. aberro* are complete and detailed, but comparison to other taxa is premature until more material becomes available for examination. Detailed analysis of the

maxillipeds of all *Paranamixis* species are required to confirm the condition of the inner plates.

Habitat. Unknown.

Distribution. East China Sea, Shijiki Bay, west Kyushu, Japan.

Paranamixis bocki Schellenberg, 1938

Paranamixis bocki Schellenberg, 1938: 29–30, fig. 14; ?Ruffo, 1969: 13. (not) Ledoyer, 1978: 231–232, fig. 14; and 1967: 125.

Diagnosis. Gnathopod 2, coxa with sharp anteroventral projection; basis serrate proximally; pereopod 5, basis quadrate.

Description. Schellenberg originally described this species from reefs in the Gilbert Islands, but his description and figures are limited and not adequate to distinguish this species from other material in hand. Until material is available from, or near, the type locality, distinguishing characteristics for this species are limited to those of the diagnosis.

Leucomorphs. Unknown.

Remarks. The author has in hand a single damaged specimen of *Paranamixis* from Truk Lagoon in the Carolines that closely resembles *P. bocki* in several features. However, due to the poor quality of this specimen and that these two regions are separated by more than 2,000 miles, they cannot be assumed to be equivalent until comparisons can be made with material collected at or near the type locality.

Habitat. Coral reefs.

Distribution. Pacific Ocean, Gilbert Islands.

Paranamixis clarkae n.sp.

Fig. 23

Type material. HOLOTYPE, anamorph male "R", 3.06 mm, USNM 243342, Mahe, Seychelles, near Mahe Beach Hotel, sheltered embayment, rubble and stones among algal turf in current swept channel, 0.5 m, J. Clark, 29 April 1984, J.Sey-2; 1 PARATYPE, anamorph male "P", 3.15 mm, USNM 243343, J.Sey-2; 1 PARATYPE, anamorph male "S", 2.69 mm, USNM 243344, J.Sey-2.

Diagnosis. Head with ventral cusp; ventral keel bifid; gnathopod 2, coxa with sharp anteroventral tooth, basis with proximolateral and mesodistal serrate ridges.

Description. Lateral margin of head rounded, anterior margin rounded, ventral margin with cusp, eyes composed of 16 compact ommatidia; ventral keel sharp, bifid, projecting anteriorly. Antennae 1 and 2, 0.94 and 0.87 as long as head to posterior margin of pereonite 4. Antenna 1, ratio of articles 1–3, 55:38:28; article 3 thin; flagellum with 8-articulate, aesthetascs on articles 4–8. Antenna 2, flagellum short, 5-articulate. Lower lip lobes visible from lateral view. Maxilliped, inner plates fused basally, but with apical notch; outer plates lacking inner lobes; palp article 4, 1.4 times length of article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1, coxa not reaching bottom margin of head, anteroventral corner rounded, bearing 2 small setae; remainder of gnathopod lacking in holotype. Gnathopod 2, coxa larger than either 3 or 4, with sharp midventral projection, scattered submarginal setae; basis, locking ridge serrate on both lateroproximal and mediodistal margins; carpus basally thick, tapering toward apex; propodus, apex defined by single sharp process lacking cusps or serrations, hindmargin nearly straight; dactyl tuberculate on inner margin. Pereopods 3 and 4 similar, coxa 4 larger than 3, posterior margin slightly expanded. Pereopods 5–6 similar, coxa 6 with deeper hind lobe than coxa 5; bases with distal portion of posterior margin excavate. Pereopod 7, coxa entire; posterior margin of basis with small serrations. Epimera normal for genus. Outer ramus of uropods 1–3 reduced, styliform and spinose; uropod 3 with small subapical spine near distal ramal spine. Telson subrectangular, tapering distally, 1.2 times longer than wide, with 2 apical setae.

Leucomorphs. Unknown at this time. Because there are at least two species of anamixids from the same locality in the Seychelles, specific designations cannot be made. Confirmation must be made through rearing experiments or through host confirmation.

Variations. Paratype "P" with shrunken vestiges of gnathopod 1, assumed to be transformation stage. Post-transformational males lack this appendage entirely. Occurrence of a vestigial first gnathopod may be a common feature of in transformational moults of *Paranamixis* as more collections are made from tropical areas. A similar condition has been noted on *P. kanu* and is probably due to the availability of more material for examination from tropical collecting efforts.

Etymology. Named in appreciation of Janice B. Clark of the National Museum of Natural History, whose untiring assistance on reefs of the Caribbean and South Pacific has been greatly appreciated.

Remarks. *Paranamixis clarkae* most closely resembles *P. excavatus* from Madagascar in the following characters: serrate locking ridges of the basis and tuberculate inner margin of the dactyl of gnathopod 2. The configuration of the basis of pereopod 5 also appears similar to that of *P. excavatus*. *Paranamixis excavatus* differs from *P. clarkae* in the more transverse anterior margin of the head, in having compact ommatidia, in lacking the prominent serrate anteroventral process on coxa 2 and in possessing ramal spines on uropods 1–3. *Paranamixis*

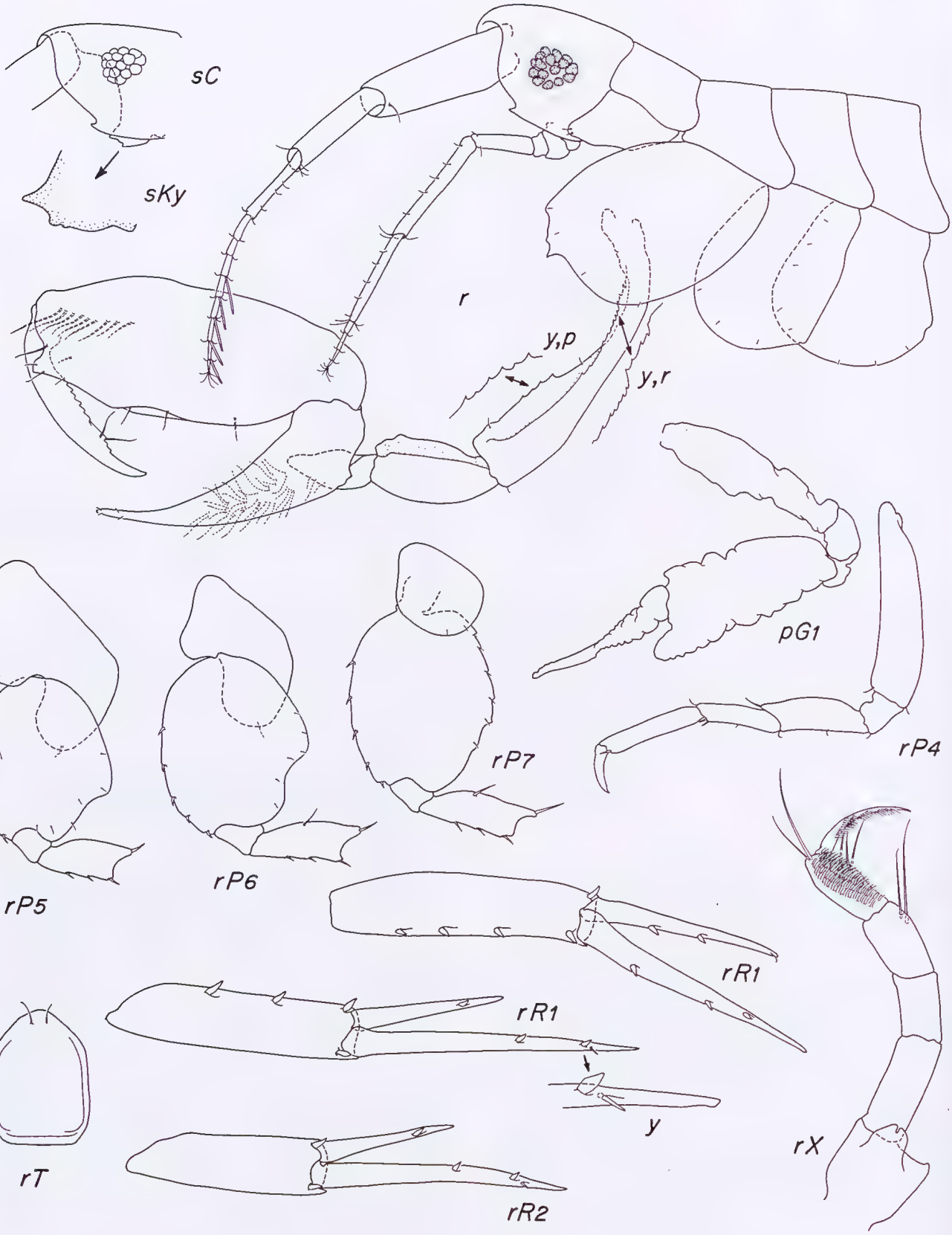

Fig. 23. *Paranamixis clarkae* n.sp., holotype, male "R", 3.06 mm; "P", anamorph male, 3.15 mm; "S", anamorph male, 2.69 mm.

clarkae is distinguished from its other nearest geographic relative *P. madagascarensis* by the following: in gnathopod 2, by the ventral projection on the coxa, the presence of serrate locking ridges on the basis, and the palm of the propodus lacking 2 additional processes. *Paranamixis indicus* from coastal India has a transverse anterior head margin and a rounded coxa 2 lacking ventral cusps or projections. *Paranamixis bocki*, the only other species in the genus with serrations on the basis of gnathopod 2, has much more apically produced cusp on coxa 1, and the basis of pereopod 5 is nearly square. Like *P. clarkae, P. indicus* from sponges in the Gulf of Manaar, India, lacks spines on the peduncles and rami of uropods 1–3, but otherwise apparently shares no close relationship to *P. clarkae*.

Habitat. Shallow coral rubble and algal turf, 1–2 m, assumed to be commensal.

Distribution. Indian Ocean; Mahe, Seychelles, 1–2 m.

Paranamixis denticulus Kim & Kim, 1991

Paranamixis denticulus Kim & Kim, 1991: 15–16, figs 2–3, depth unrecorded.

Diagnosis. Anterior margin of head oblique, with midventral notch. Gnathopod 2, anterior margin of coxa smooth, lacking cusp(s) or tooth, inner margin of dactyl with 4–5 distinct tubercles.

Remarks. The midventral notch on the head and finely denticulate margin of the propodus of gnathopod 2 place *P. denticulus* among the other Asian taxa exhibiting these features, *P. misakiensis* and *P. aberro*. Differences among these taxa are generally found on the anterior margin of coxa 2 and the presence and type of tubercles on the inner margin of the dactyl of gnathopod 2.

Habitat. Coral rubble and rocky bottoms, shorelines and harbours.

Distribution. Sea of Japan, Ulreung Island.

Paranamixis excavatus Ledoyer, 1978

Paranamixis excavatus Ledoyer, 1978: 233, fig. 14 (I).

Diagnosis. Anterior margin of head nearly transverse, anteroventral margin defined by small cusp, ommatidia reduced in number, scattered and diffuse, ventral keel subtriangular, projecting beneath head. Gnathopod 2, anteroventral margin of coxa produced into sharp process, proximal margin linear, serrate; basis with serrate lateral ridge and serrate distal locking ridge; propodus elongate and thin, with single large tooth near dactyl. Rami and peduncles of uropods lacking spines; telson ovate.

Remarks. There is little additional information available from Ledoyer's description of *P. excavatus*. The description is only three sentences in length and the figures consist of nine separate drawings. Nonetheless, this unusual species is readily distinguishable from all other *Paranamixis* by the scattered and diffuse ommatidia; ventral process and serrations on coxa 2; and the complete loss of spines on the peduncles and rami of the uropods. The outer ramus of uropod 1 is reduced to half of the inner ramus. Detailed examination of this species is certain to provide additional taxonomic characters overlooked in the original description. Specialised collecting efforts in the waters or Mauritius may also be expected to provide additional undescribed anamixid species.

Habitat. Unknown.

Distribution. Indian Ocean, Mauritius, coral reefs, to 5 m.

Paranamixis fijiensis n.sp.

Fig. 24

Type material. HOLOTYPE, anamorph male "A", 2.87 mm, USNM 266410, *Halimeda* in lagoon, Nanaui Ra, Fiji, 6 October 1979, Alan Myers, station 53. PARATYPES, anamorph males "B", 2.92 mm, USNM 266411, and "C", 2.72 mm, USNM 266412.

Diagnosis. Gnathopod 2, coxa enlarged, anteroproximal margin expanded; basis with weakly denticulate anterodistal locking ridge, propodus extending proximally beyond insertion of carpus. Maxilliped, inner plates fused, apically rounded. Telson elongate, 1.9 times longer than wide.

Description. Holotype "A". Head, anterior margin more or less transverse, somewhat expanded, anteroventral corner defined by small cusp; ventral keel scarcely extending beneath ventral margin of head, triangular; eyes with 21 compact ommatidia. Antennae: antenna 1 peduncular ratio 25:20:14; flagellum 7-articulate, aesthetascs on articles 5–7; antenna 2, flagellum 4-articulate. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.6 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1 lacking, coxa reduced, apically bifid. Gnathopod 2, coxa larger than 3 or 4, anteroproximal expanded, ventral margin evenly rounded, posterior margin with small cusp; basis with serrate anterodistal locking ridge on medial margin; carpus recurved, tapering distally, unarmed; propodus, proximal margin extending beyond insertion of carpus, hindmargin unarmed, furnished with approximately 7 submarginal setae, distal margin with small serrations;

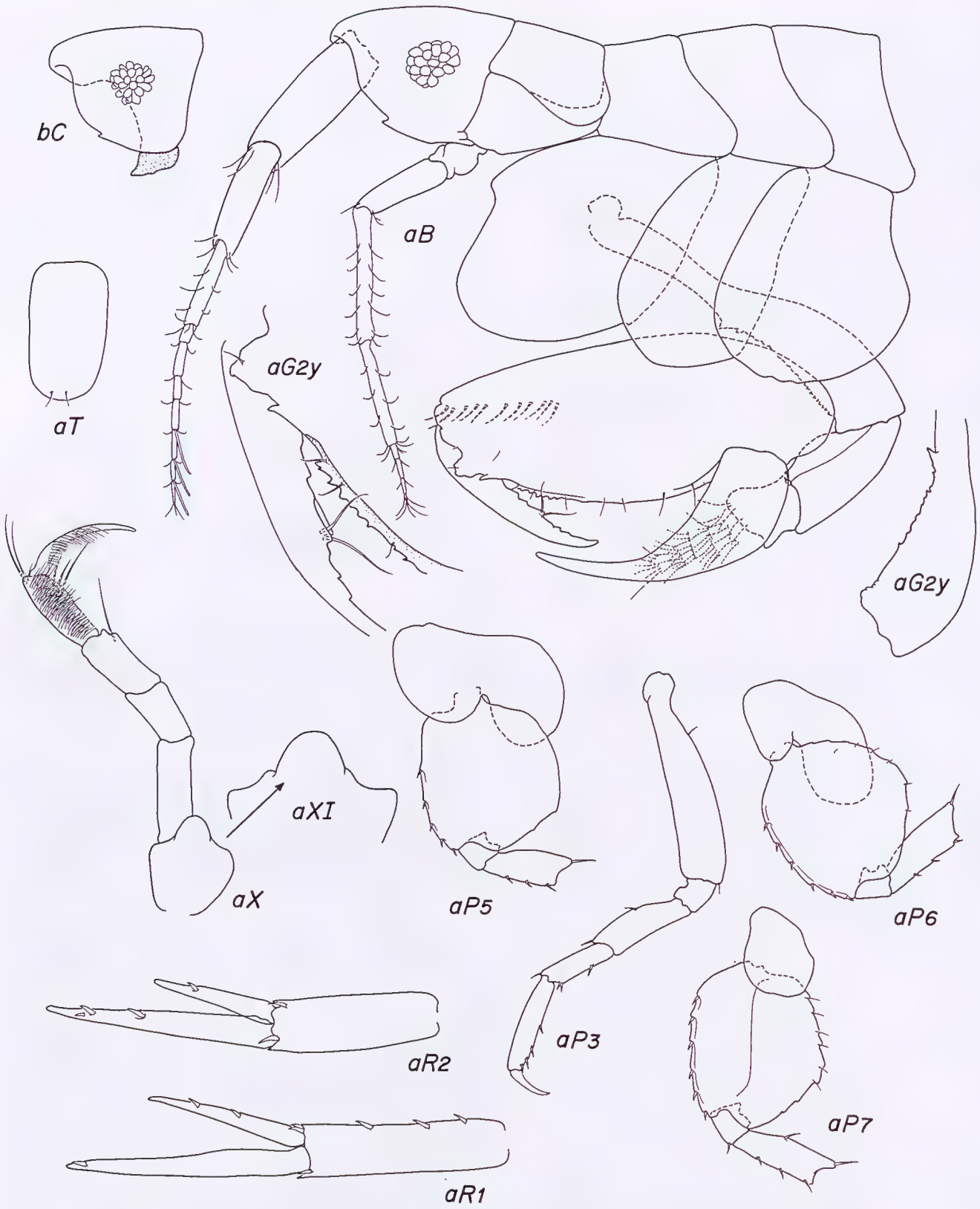

Fig. 24. *Paranamixis fijiensis* n.sp., holotype, anamorph male "A", 2.87 mm; "B", 2.92 mm.

dactyl with 4–5 widely spaced serrations on inner margin. Pereopod 3, coxa smaller than 4, ovorectangular, ventral margin expanded. Pereopod 4, ventral margin of coxa expanded, with 2 small emarginations. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, with widely separated serrations bearing submarginal setae. Pereopod 7, coxa oval. Uropods 1–2, outer rami shortened, two-thirds and one-half of inner rami respectively. Uropod 3 missing. Telson entire, elongate and subrectangular, 1.9 times longer than wide, apical margin rounded, with pair of apicodistal setae.

Leucomorphs. Unknown. The report by Myers (1985) of a leucomorph from Fiji cannot be attributed to *P. fijiensis* until a more thorough survey of the anamixid fauna is made.

Etymology. Named for the Island nation of Fiji.

Relationships. *Paranamixis fijiensis* appears to be similar in several respects to *P. madagascarensis*, including the general shape of the head, gnathopod 2, and coxae 3–4. *Paranamixis fijiensis* is distinguished within *Paranamixis* by the anteroproximal expansion of coxa 2 and the apically fused inner plates of the maxilliped.

Remarks. Until the discovery of *P. fijiensis*, all previously examined species of *Paranamixis* had apically cleft or partially fused inner plates of the maxilliped. The elongate telson of *P. fijiensis* is morphometrically identifiable with the genus *Nepanamixis*, however, it is ovorectangular in *P. fijiensis*, not apically tapered as is typical in *Nepanamixis*. These apparent anomalies are examples of mosaic characters that seem to arise in isolated or relict anamixid species, such as *A. aldabra* and *N. torreanus*. Isolation appears to contribute to this unusual mix of plesiomorphic and apomorphic traits. Again, the cautionary note of incomplete collections, taxonomies and analysis, must be invoked, reflecting our incomplete understanding of the group. In the case of *P. fijiensis* the apically fused inner plates of the maxilliped present two possibilities: (1) a species of *Paranamixis* with fused inner plates on the maxilliped, or (2) a form of *Anamixis* that has lost gnathopod 1. The vestigial first gnathopod of *A. jebbi* may be a transitional example of how this appendage is lost, by gradual reduction rather than immediate developmental loss. Further investigations may resolve whether loss of gnathopod 1 may have arisen in multiple anamixid lineages.

Habitat. Unknown, presumed to be commensal.

Distribution. South Pacific Ocean, Nananui, Fiji, coral reefs, lagoonal.

Paranamixis indicus Sivaprakasam, 1968

Paranamixis indicus Sivaprakasam, 1968: 131–136, figs 1–3; (not Ledoyer, 1978: 233).

Diagnosis. Ventral keel truncate; propodus of gnathopod 2 with deep sinus near articulation with carpus; peduncles and rami of uropods lacking spines.

Description. Head, anterior margin transverse, lower margin defined by small upturned tooth; eyes with 20–22 ommatidia; ventral keel a truncate process angled forward. Antenna 1, ration of articles 1–3, 11:12:6. Gnathopod 2, coxa larger than 2 or 3, rounded, anterior margin with 2 teeth; propodus, palm undefined and continuous with hindmargin, with flat-topped tooth near base of dactyl, followed by a small, pointed tooth with a seta, followed by a shallow sinus and then a small and a minute tooth, remainder of hindmargin straight with 5 equidistant setulae, base with a narrow sinus; dactyl about half as long as propodus, curved near the base and near the pointed tip, the middle portion being straight; proximal two-thirds stout, inner margin with small tooth at curve near the base, followed by a series of eight teeth gradually increasing in size with 2 setae on teeth 7 and 8; distal one-third of dactyl half as thick as the rest, with 4 teeth on inner margin. Coxa 4 larger than 3, posterior margin expanded. Telson entire, apex broadly rounded, 1.33 times longer than wide.

Leucomorphs. Unknown.

Relationship. *Paranamixis indicus* and *P. excavatus* both have uropods completely lacking spines, but share virtually no other similarities. The truncate ventral keel of *P. indicus* is also unusual for this genus, the process being triangular in those species where it has been described.

Remarks. It is doubtful that the loss of spines on the uropods of *P. indicus* link it to *P. excavatus* in an evolutionary perspective, because each species may have evolved this condition independently. A similar convergence is seen in the laterally excavate head margins of *P. kanu* and *A. vanga*.

Habitat. Occurring in sponges, leucomorphs undocumented.

Distribution. Indian Ocean, Appa Island in the Gulf of Manaar, Madras, India, littoral.

Paranamixis kanu n.sp.

Fig. 25

Type material. HOLOTYPE, anamorph male "A", 3.77 mm, USNM 243345, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble 50 m south of reef marker, 3–4 m, J.D. Thomas, 2 February 1990, JDT-PNG-32b; 1 PARATYPE, anamorph male "B", 3.70 mm, USNM 243346, JDT-PNG-32b; 8 PARATYPES, USNM 243347, JDT-PNG-32b; 15 PARATYPES, USNM 243348, JDT-PNG-50c; 11 PARATYPES, JDT-PNG-51a, USNM 243349

Diagnosis. Lateral margin of head excavate, anterior margin oblique; inner plates of maxilliped cleft, apically sharp. Coxae 2 larger than 3 or 4; margins of coxae evenly rounded, bearing submarginal setae. Propodus of gnathopod 2, hindmargin with serrate subdistal process followed by 2 smaller projections; inner margin of dactyl tuberculate.

Description. Head, lateral margin excavate below prominent lateral ridge, ventral margin oblique, eye with 23 compact ommatidia, ventral keel barely extending

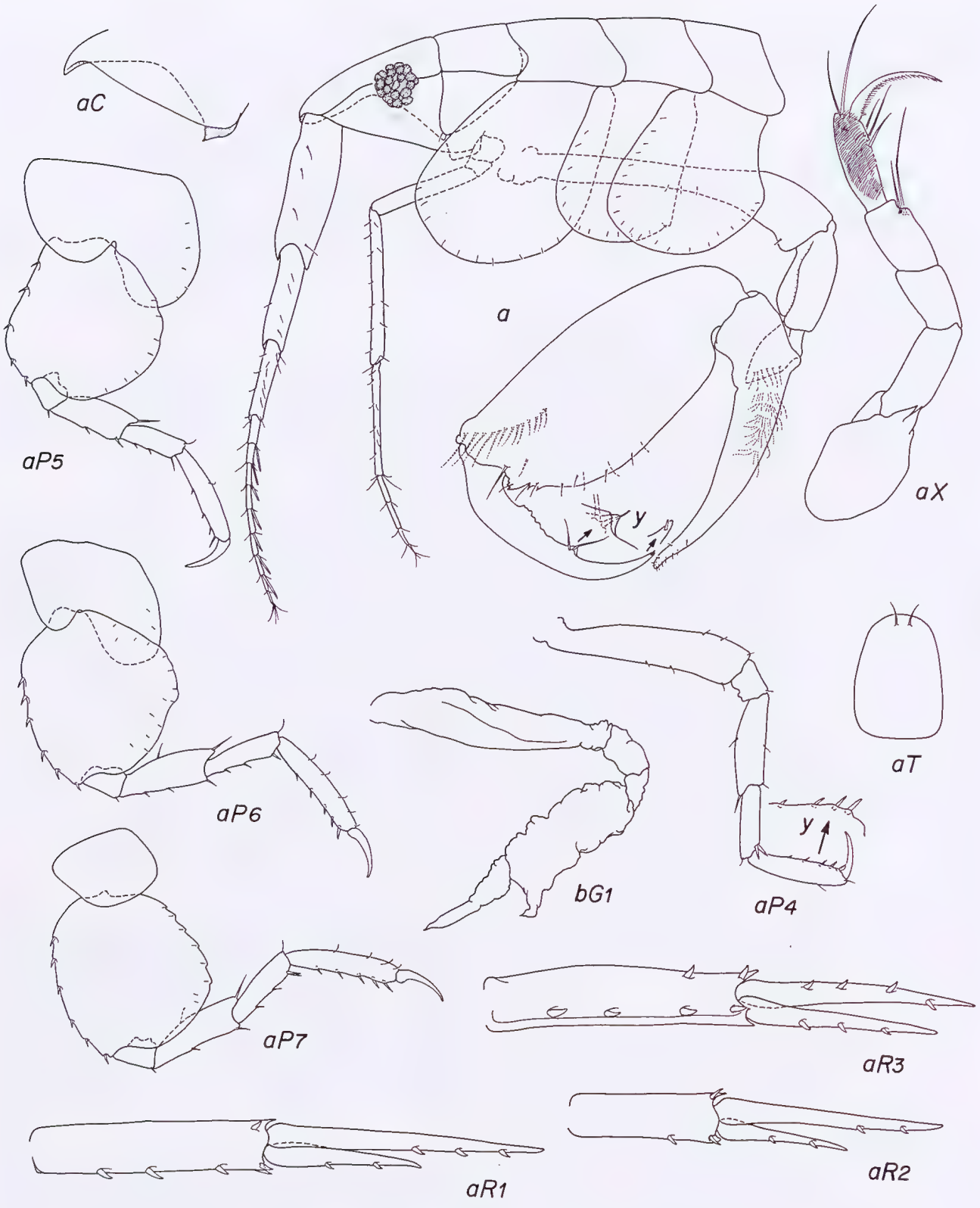

Fig. 25. *Paranamixis kanu* n.sp., holotype, male, "A", 3.77 mm; "B", anamorph male, 3.70 mm.

below head, anterior margin apically pointed. Antennae long, antennae 1 and 2, 1.0 and 1.03 as long as head to pereonite segment 4. Antenna 1, ratio of articles 1–3, 48:35:26; flagellum 9-articulate, aesthetascs on articles 1–7. Antenna 2, flagellum short, 4-articulate. Maxilliped, inner plates partially fused, apices sharp; outer plates lacking inner lobes; palp article 4, 1.05 times longer than article 3. Pereonite 1, prominent lateral locking ridge present. Gnathopod 1, coxa reduced, not reaching bottom margin of head, apex rounded with 2 setae;

remainder of gnathopod absent. Gnathopod 2, coxa larger than 2 or 3, margins smooth, ventral margin expanded, with numerous submarginal setulae; basis with 3 short setae near midpoint; carpus, apex slightly recurved, furnished with short setae on inner and outer margins; propodus, hindmargin slightly expanded, distal portion with large serrate process and 2 smaller posterior teeth; dactyl recurved, proximal portion with raised tuberculate ridge, distal third with paired setae between 2 projections. Pereopod 3, coxa smaller than 4, margins not expanded, with numerous posterior and ventral submarginal setulae. Pereopod 4, coxa with ventral and posterior margins slightly expanded, smooth, with numerous anterior and ventral submarginal setulae. Pereopod 5, coxa with hind margin slightly produced; basis subcircular, posterior margin smooth. Pereopod 6, coxa with hind lobe greatly produced; basis subcircular with slight excavation below mid-posterior margin. Pereopod 7, coxa entire, basis subcircular, posterior margin with series of notches. Epimera normal. Uropods 1 and 2, outer rami shortened, spinose. Uropod 3, outer ramus slightly shortened. Telson subrectangular, apically rounded, 1.4 times longer than wide, with pair of apical setae.

Leucomorphs. Unknown.

Variations. Anamorph male "B": gnathopod 1 present as small shrivelled appendage on what is assumed to be a transformational moult, otherwise, gnathopod 1 lacking in all post-transformational moults.

Relationship. *Paranamixis kanu* bears no close resemblance to other species of *Paranamixis* due to the oblique anterior angle, and midlateral ridge of the head.

Etymology. The word kanu, is Riwo pidgin for canoe and it refers to the shape of the head that looks similar to the upturned bow of local outrigger canoes.

Remarks. A common species, host(s) unknown. Other anamixids with laterally excavate heads are known to inhabit larger solitary ascidians (sponges?) where the lateral ridge serves to anchor the head against the second coxa while feeding in the increased current velocities generated by larger hosts.

Habitat. Coral rubble.

Distribution. South Pacific Ocean; north and south coasts of Papua New Guinea; northern Queensland, to 5 m.

Paranamixis madagascarensis Ledoyer, 1982

Paranamixis madagascarensis Ledoyer, 1982: 141–142, fig. 49. Not Myers, 1985: 42–44, fig. 31.

Diagnosis. Rami of uropods 1 and 2, one-half the length or less than inner rami. Gnathopod 2, basis with denticulate distolateral ridge; dactyl deeply excavate near base, inner margin denticulate to apex.

Description. Head, anterior margin produced, then tapering to small cusp. Antenna 1, ratio of articles 1–3, 12:7:4; accessory flagellum minute, 1-articulate, tipped with a seta; flagellum 9-articulate. Antenna 2, flagellum 4-articulate. Gnathopod 2, coxa larger than 3 or 4, rounded, lacking cusps, anterior margin slightly produced; propodus, palm undefined, hind margin with 1 large and 2 small teeth; dactyl nearly straight, deeply incised near base. Coxa 3 smaller than 4. Telson subrectangular, apex more or less truncate, 1.33 times longer than wide.

Leucomorphs. Unknown.

Relationship. *Paranamixis madagascarensis* differs from its closest relative *P. indicus* in lacking anteroproximal teeth on coxa 2, the presence of a denticulate distolateral ridge on the basis of gnathopod 2, and the more reduced outer rami with spines on uropods 1 and 2.

Remarks. Myers report of *P. madagascarensis* from Fiji is *P. fijiensis*.

Habitat. Coral rubble.

Distribution. Indian Ocean, Madagascar to Mauritius, coral reefs, 0–4 m.

Paranamixis misakiensis n.sp.

Fig. 26

Type material. HOLOTYPE, anamorph male "M", 4.41 mm, CRU1575, deposited in the Zoological Museum, Copenhagen, Denmark, Misaki Coast, Sagami Bay, Japan, on *Corallina*, littoral collections and dredging to 20 fathoms, Th. Mortensen, 26 May 1914.

Diagnosis. Head, anterior angle oblique, bearing midlateral notch. Maxilliped, inner plates fused except for small apical notch. Gnathopod 2, anterior margin of coxa expanded, with small, truncate cusp; basis with toothed, distomedial locking ridge; carpus reaching half of propodus, anterior margin minutely toothed; hind margin of propodus expanded, evenly serrate; inner margin of dactyl tuberculate.

Description. Holotype "M". Head, anterior margin oblique, bearing midlateral notch; ventral keel a simple triangular process barely extending below ventral margin of head; eyes with 22 compact ommatidia. Antennae: antenna 1, peduncular ratio 22:13:9; accessory flagellum minute, 1-articulate; flagellum 10-articulate, aesthetascs on articles 2–10; antenna 2, subequal or slightly longer than antenna 1, peduncle article 3 elongate, 0.87 as long as article 4; flagellum 4-articulate. Maxilliped, inner plates almost completely fused, apical margin minutely cleft; outer plates lacking inner lobes; palp article 4, 1.1 times article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1 lacking, coxa reduced, apically bifid.

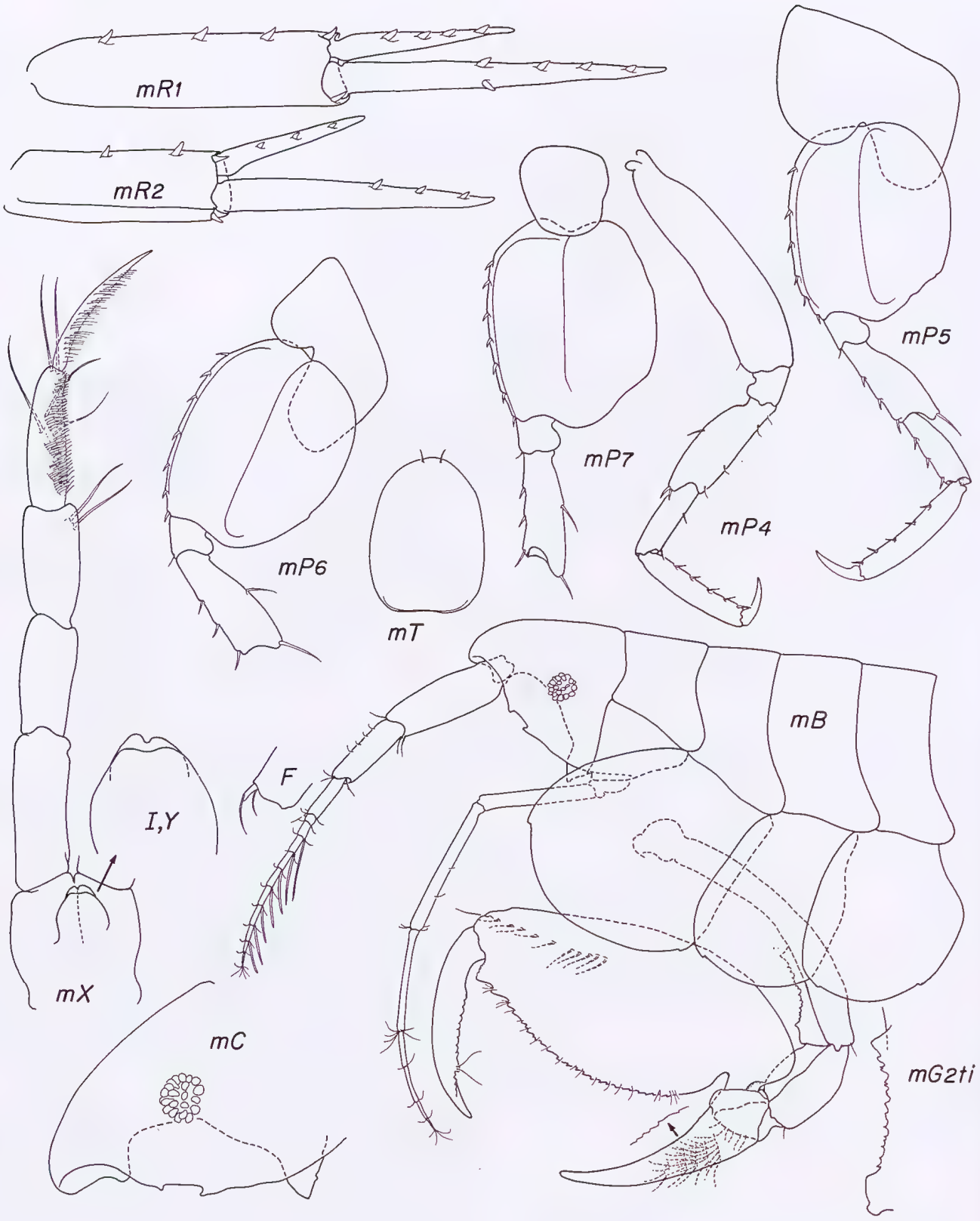

Fig. 26. *Paranamixis misakiensis* n.sp., holotype anamorph male "M", 4.41 mm.

Gnathopod 2, coxa much larger than 3 and 4, anterior margin rounded, with truncate cusp; basis with serrate distomedial locking ridge; carpus short, slightly recurved, reaching 0.50 of propodus, anterior margin with minute serrations; hindmargin of propodus expanded, evenly serrate, with scattered submarginal setae; inner margin of dactyl with small tubercles. Pereopod 3, coxa ovorectangular, subequal in size to 4, anteroventral

margin with cusp. Pereopod 4, ventral margin of coxa rounded, anteroventral and posteroventral corners with small cusp. Pereopod 5–6 similar, coxae bilobed; bases with spinose anterior margins, posterior margins without submarginal setae. Pereopod 7, coxa entire basis similar to pereopods 5 and 6. Uropods 1 and 2, outer rami reduced approximately one-half of inner. Telson broad, entire, distal margin rounded, 1.3 times longer that wide, single pair of apical setae.

Leucomorphs. Unknown.

Etymology. Name refers to the Misaki Coast, Japan.

Relationship. *Paranamixis misakiensis* is most closely related to *P. aberro* from Shijiki Bay, Japan in the transverse anterior angle of the head with a midlateral notch; the small, triangular ventral keel; and the elongate peduncle article 3 of antenna 2. *Paranamixis misakiensis* differs from *P. aberro* primarily in features of gnathopod 2, including a cusp on the anterior margin of the coxa; the presence of a serrate distomedial ridge on the basis; the shortened carpal lobe; and the serrate hindmargin of the propodus; and the tuberculate inner margin of the dactyl. *Paranamixis misakiensis* also lacks submarginal setae on the posterior margin of the basis on pereopods 5–7.

Remarks. *Paranamixis misakiensis* and *P. aberro* appear to be more similar to each other than either species is to any other species of *Paranamixis*, a relationship not confirmed by cladistic analysis. Examination of existing material, and the collection of new material from Japanese and Asian waters will expand the species diversity of anamixids in this region. The presence of minutely cleft inner plates of the maxilliped is significant in a taxonomic and evolutionary sense, but its relevance must await detailed examination of this character in other taxa.

Habitat. Presumed commensal, specific host(s) unknown.

Distribution. Sagami Bay, Pacific Ocean, on *Corallina*.

Phylogenetic analysis

Relationships among and within the genera *Anamixis, Paranamixis* and *Nepanamixis* were analysed using HENNIG86 by James Farris. Analyses of *Anamixis* and *Nepanamixis* were based on data presented in the character matrix, with 41 characters and 24 taxa. Kevin Nixon's CLADOS program was used to map and view characters on the resulting trees. The cladistic analysis was run using the genus *Leucothoe* as the outgroup. All multistate characters were treated as unordered and nonadditive. The analysis in HENNIG86 included a successive weighted option (XS W) and the M*BB* which incorporates branch swapping and uses all available tree space to store results. Initial analyses using all taxa resulted in 16 equally parsimonious trees with a consistency index of 0.81. Many of the characters used in the analysis could not be coded for the genus *Paranamixis* due lack of material for observation. Because the condition of the inner plates of the maxilliped are critical, and, except for *Paranamixis* species described herein, no material is available for analysis. The largest amounts of variability within the cladograms was due to *Paranamixis*. Since *Paranamixis* appeared to be obscuring a more succinct analysis, it was omitted and subsequent analyses were made with *Nepanamixis* and *Anamixis* for which most taxa were able to be completely scored, with the exception of *A. stebbingi* and *A. yarrega*. Analysis of *Anamixis* and *Nepanamixis* produced 12 equally parsimonious trees with a consistency index of 0.85 which were then used to generate a strict consensus tree. This cladogram is represented in Figure 27.

The discussion of generic and specific relationships is organised by nodes labelled in the cladogram, Figure 27. Supporting characters for each node are discussed, the character number is listed above the small rectangle, the character state below. Homoplastic characters are represented by a small dark rectangle below the box.

The character matrix used to score characters and character states is listed below.

Character matrix

1. Eyes: number of ommatidia
   0 = 10+
   1 = 9
   2 = 7
2. Antennae, relative to body length
   0 = both antenna 1, antenna 2 short, less than 1/2 body length
   1 = antenna 1, antenna 2 greater than 1/2 body length
3. Head size
   0 = head less than pereonites 1,2
   1 = head greater than pereonites 1–2
4. Head, anterior margin
   0 = rounded, no notch anteroventral corner
   1 = oblique, unadorned
   2 = oblique, with midlateral notch
   3 = transverse
   4 = oblique, with anteroventral notch
5. Head, lateral margin
   0 = evenly rounded
   1 = with prominent lateral ridge
6. Ventral keel, shape
   0 = sharp
   1 = rounded/truncate
   2 = sharp, with anterior serrations/teeth
   3 = rounded, with anterior teeth
7. Maxilliped, inner plates
   0 = inner plate spinose, lobes separate
   1 = inner plate without spines, cleft to base; outer plate with inner lobes
   2 = inner plate without spines, cleft 1/2–1/3; outer plate with vestigial inner lobes

3 = inner plate without spines, cleft 1/2–1/3; outer plate without inner lobes
4 = inner plate without spines, apically notched or truncate; outer plate without lobes
5 = inner plate without spines, apically rounded; outer plate without lobes

8. Maxilliped, palp article 4
0 = short, not recurved
1 = recurved, 1.0–1.8 × article 3 (normal)
2 = recurved, 1.9+ × article 3 (elongate)

9. Coxa 1
0 = coxa 1 subequal to coxae 2–4, apically rounded
1 = coxa 1 one-half of coxa 2, apically rounded
2 = coxa 1 less than one-quarter coxa 2, apically bifid

10. Gnathopod 1 (revised)
0 = carpochelate, article 6 greater than 5
1 = carpochelate, article 6 not equal to 5; no terminal seta(e)/spine
2 = carpochelate, article 6 not equal to 5; with terminal setae/spine
3 = article 5 basally inflated
4 = article 5 distally attenuate
5 = article 5 distally expanded
6 = gnathopod 1 vestigial
7 = gnathopod 1 absent (*Paranamixis*)
8 = article 5 moderately inflated, with terminal spine

11. Antennae 1, peduncle
0 = peduncle article 1 of normal thickness, width less than 2.0 × article 2.
1 = peduncle article 1 substantially enlarged/thickened: width greater than 2.0 × article 2

12. Antennae, relative length of antenna 1–2
0 = antenna 1 = antenna 2
1 = antenna 1 greater than antenna 2

13. Coxa 2: relative size versus coxa 3–4
0 = coxa 2 = coxa 3–4
1 = coxa 2 (occasionally 3) enlarged greater than 3 or 4, moderately enlarged
2 = coxa 2 greatly enlarged, 2.0 × coxa 3 or 4

14. Coxa 2, anterior margin
0 = small, evenly rounded
1 = with small cusps/teeth
2 = with large cusps/processes
3 = medial portion broadly expanded

15. Gnathopod 2, ornamentation of basis
0 = unarmed
1 = tuberculate proximal ridge
2 = serrate distal ridge (*Paranamixis*)
3 = numerous long setae present

16. Gnathopod 2, carpal lobe
0 = short, less than one-half of palm
1 = long, straight, wide at base; reaching apex of propodus
2 = medium, thickened basally, blunt, not reaching apex of propodus
3 = long, recurved, depth greater than one-half of palm, thin reaching 2/3 of propodus
4 = long; geniculate, reaching nearly to end of propodus.

17. Gnathopod 2, carpus, ornamentation
0 = unornamented
1 = bifid process or denticles
2 = serrate lateral ridge

18. Gnathopod 2, mediofacial setae on propodus
0 = 1 long row of mediofacial setae
1 = 2 long rows of mediofacial setae
2 = 2 rows of mediofacial setae; 1 long, 1 sparse

19. Gnathopod 2, general morphology
0 = Type I =carpus short, grooved, palm oblique, dactyl less than one-half of palm
1 = Type II =carpus short, palm oblique, dactyl recurved, reaching one-half along palm
2 = Type III =carpus long, straight, propodus 2.5 × longer than wide, dactyl straight, one-half length of palm
3 = Type IV =carpus long, recurved, propodus thin, greater than 3.4 × longer than wide; dactyl long, geniculate
4 = Type V =carpus short, palm oblique, with major teeth, dactyl reaching end of propodus

20. Gnathopod 2, ornamentation on propodus
0 = oblique, generally lacking significant ornamentation
1 = truncate, no teeth or cusps
2 = few teeth/cusps, shape variable
3 = major teeth/excavations
4 = entire hindmargin with small serrations
5 = with medial cusps/process

21. Gnathopod 2, dactyl
0 = medium length, recurved, unarmed
1 = medium length, recurved, with serrations, tubercles or ridges
2 = long, evenly recurved
3 = long, geniculate
4 = long, apically bifid

22. Coxa 3, anterior margin
0 = straight, evenly rounded
1 = expanded anteriorly

23. Coxa 4, ventral margin
0 = evenly rounded
1 = crenulate/produced
2 = excavate

24. Uropods, length
0 = rami equal
1 = outer ramus of uropods 2–3 one-half of inner

25. Uropods, spination
0 = spinose
1 = lacking spines

26. Telson, length
0 = 2.5 × width (long)
1 = 1.8–2.0 × width (intermediate)
2 = less than 1.7 × width (short)

27. Coxa 2, ventral margin
0 = rounded
1 = produced; rounded or angular
2 = sinuous; with large cusp
3 = small cuspate process
4 = excavate
5 = anteroventral corner produced

28. Gnathopod 2, proximal margin of carpus
0 = smooth, unarmed
1 = denticulate/serrate

29. Gnathopod 1, article 6
0 = normal, curved (absent in *Paranamixis*)
1 = geniculate

30. Telson shape
    0 = triangular
    1 = broad, ovate
31. Juvenile morphology
    0 = juveniles and females similar to adult males
    1 = juveniles and females dissimilar to adult males
32. Juvenile, gnathopod 1
    0 = carpochelate, 7 articulate
    1 = chelate, carpus less than 1/2 length of propodus, with 3 long, spoon-shaped spines, 6-articulate
    2 = chelate, carpus with single (occasionally double) spine(s)
33. Maxilliped, outer plate, palp article 1
    0 = outer plate with inner lobes, produced
    1 = outer plate without inner lobes, unproduced
34. Maxilliped, length of outer plate
    0 = prominent, reaching to end of palp article 1
    1 = reduced; reaching less than one-half of palp article 1
    2 = vestigial; scarcely produced
    3 = absent
35. Maxilliped, shape of inner plate
    0 = inner plates cleft; one-half to base
    1 = inner plate entire (apically truncate/rounded, or with small apical processes)
36. Maxilliped armament on inner plates
    0 = small spines
    1 = no spines
37. Maxilliped, apical ornamentation of inner plate
    0 = apical margin unarmed
    1 = apical margin with small projections
    2 = apical margin sharp, lobes deeply cleft
38. Gnathopod 1, apical ornamentation on dactyl
    0 = none
    1 = long seta(e)
    2 = swollen knob, small nipple
39. Gnathopod 1, gross morphology (transformed males)
    0 = carpochelate
    1 = chelate
    2 = vestigial
    3 = absent
40. Gnathopod 1, shape of dactyl
    0 = linear
    1 = geniculate
41. Gnathopod 2, insertion point article 5
    0 = insertion point at a more proximal margin of article 6
    1 = insertion point at one-third of article 6 (verticalised)

Node A: *Nepanamixis*.—This genus is supported by ten apomorphic characters, four of which demonstrate some degree of homoplasy. Characters 1,7,9,10,18,32 and 38 provide unambiguous support, while characters 17,21 and 37 are ambiguous. Character 32 has been documented only in *N. dianthus* and is inferred in the remaining taxa of the clade. Clearly while there is homoplasy within this node, there are clearly apomorphic characters that unite these taxa into a monophyletic clade.

Character 1: number of ommatidial facets in the eyes.—The genus *Nepanamixis* is unique in having nine ommatidial facets (state 1). This character is also documented in the only described juvenile morphology, *N. dianthus*. For the other members of the genus, this character is known only from adults.

Character 7: inner plates of maxilliped.—All taxa in this group have the inner plates of the maxilliped cleft one-half or more to the base (state 1).

Character 9: relative size of coxa 1 to coxae 2–4.—The apomorphic condition of coxa 1 being approximately one-half the size of coxae 2–4 (state 1) is unequivocal for these taxa.

Character 10: shape of gnathopod 1.—The basal portion of gnathopod 1 is inflated in *Nepanamixis*, (state 3) providing a distinct morphology for this appendage.

Character 17: ornamentation of carpal lobe, gnathopod 2.—The presence of a serrate lateral ridge (state 2) along the carpal margin distinguishes three of the four taxa in this group.

Character 18: rows of mediofacial setae on propodus of gnathopod 2.—The presence of a double row of long mediofacial setae on the propodus (state 1) is unique to *Nepanamixis*. Other taxa either have a single long row of such setae, or a second row consisting of only a few setae.

Character 21: gnathopod 2, length and shape of dactyl.—The long, evenly recurved condition of the dactyl (state 2) is equivocal, showing much homoplasy throughout all taxon groups. The strength of this character in diagnosing relationships appears to be minimal.

Character 23: ventral margin of coxa 4.—The crenulate or produced ventral margin of coxa 4 (state 2) is a synapomorphy for two species, *N. torreanus* and *N. vectoris*.

Character 26: telson length.—All four taxa in this clade have telsons of intermediate length-versus-width ratio of 1.8–2.0 (state 1).

Character 29: telson shape.—The triangular telson (state 0) is unequivocal for all *Nepanamixis*.

Character 32: juvenile morphology of gnathopod 1.—The unusual chelate condition of juvenile gnathopod 1 with three embedded, spoon-shaped spines in article 6 is known only from *N. dianthus* from Belize, and hypothesised for the sister species *N. grossimana* and eastern Pacific taxa, *N. torreanus* and *N. vectoris*. Whether other members of this group have similar juvenile morphologies remains to be resolved.

Character 37: apical ornamentation of inner plate of the maxilliped.—The rounded apical margins of the inner plates and the deeply to moderately cleft nature of the inner plates (state 3) uniquely defines *Nepanamixis*.

Character 38: gnathopod 1, apical ornamentation of dactyl.—The presence of a small knob-like process at the terminus of the dactyl (state 3) is an apomorphic condition that defines the taxa at this node.

Node B: the *grossimana–dianthus* clade.—These two taxa both have long, geniculate dactyls on gnathopod 2 (character 16, state 4) and an excavate ventral margin on coxa 4 (character 23, state 2). While *N. grossimana* and *N. dianthus* are sister species, their widespread distributions, Mauritius and Belize respectively, present a disjunct pattern that is difficult to evaluate in the absence of additional material from intermediate localities. It is probable future sampling efforts will reveal related taxa.

Node C: the *Anamixis* clade.—This node is supported by eight characters, three of which are homoplastic, 4, 7 and 34. Apomorphic character support is furnished by characters 9, 30, 32 and 39.

Character 4: shape of anterior margin of head.—The shape of the anterior margin of the head exhibits varying degrees

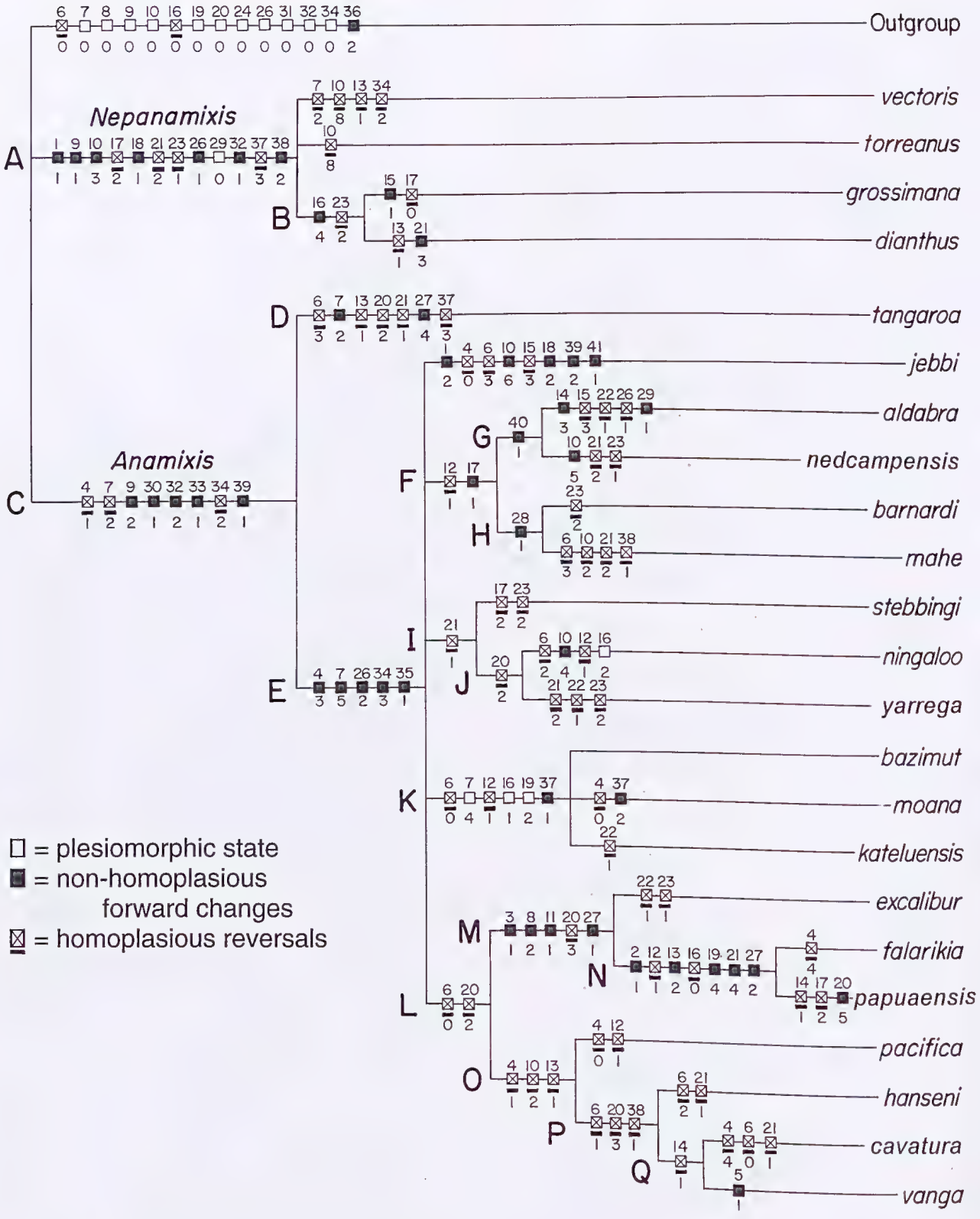

Fig. 27. Strict consensus tree of the Anamixidae.

of homoplasy and is equivocal for almost all taxa. Due to the nature and variety of homoplasy encountered, this character currently does not support monophyly.

Character 7: inner plates of the maxilliped.—With the exception of *A. tangaroa* that has cleft inner plates (state 2) and the *bazimut–moana–kateluensis* clade that has apically notched or indented inner plates (state 4), the remaining species all exhibit apically rounded plates (state 5). The ancestral condition of fully cleft inner plates (state 0) appears to be gradually lost as fusion of the inner plates results in decreasing amounts of separation.

Character 9: size of coxa 1 versus coxae 2–4.—The

synapomorphic character of coxa 1 reduced to one-quarter or less of coxae 2–4 (state 2) unequivocally defines all *Anamixis*. In all taxa that have been examined by the author the apex of the reduced coxa exhibits a small bifid process. In most cases where material was unavailable for examination and figures of extant taxa were relied upon, the bifid apex was not illustrated. It is probable that this condition was overlooked and most likely occurs in all *Anamixis* species.

Character 30: shape of telson.—The broad, ovate shape of the telson (state 1) unequivocally defines the *Anamixis* clade.

Character 32: juvenile morphology.—All *Anamixis* juveniles (leucomorphs) have chelate first gnathopods with a single embedded apical spine. This character is hypothesised for most *Anamixis* as the majority of the juvenile stages remain to be documented.

Character 33: palp article 1, outer plate of maxilliped.—Outer plates lack inner lobes in all *Anamixis*. This character is unequivocal for the node (state 1).

Character 34: maxilliped, length of outer plate.—The outer plate is absent in all *Anamixis* (state 3).

Character 39: gnathopod 1 morphology (transformed males).—Unequivocal for *Anamixis*, all anamorphs have thin, finely chelate first gnathopods (state 1) except for the vestigial gnathopod 1 of *A. jebbi*.

Node D: the "*tangaroa*" clade.—This unusual species from the cool, deep waters of the Bass Strait exhibits several characters that indicate its possible link with ancestral lineages. While seven characters that define this species, only two provide unequivocal support. Those characters are condition of the inner plates of the maxilliped (character 7) and the length of the telson (character 26).

Character 7: inner plate of maxilliped.—The inner plates of *A. tangaroa* are partially cleft, with fusion occurring along one-half to one-third the medial margin (state 2).

Character 26: telson length.—The telson is of the intermediate length (state 1). This condition is unequivocal and clearly relates *A. tangaroa* those taxa with more elongate telsons (Node A).

Node E.—This node contains the remaining members of the *Anamixis* group. In addition to the characters already discussed for *Node C* there are two characters that provide unequivocal support for this group. Telson length (character 26) and the shape of the inner plate of the maxilliped (character 35).

Character 26: telson length.—All remaining taxa in this group are united by the shortened condition of the telson (state 2). While there is some variation within this character all species have telsons 1.7X or less, width versus length.

Character 35: shape of inner plate of maxilliped.—All remaining taxa are supported unequivocally by having inner plates that are apically truncate or rounded. In the case of the Pacific Plate species (Node K), a slight emargination or projection of the apical margin is present.

Node F: Indian Ocean anamixids.—The four species in this clade, *A. aldabra, A. nedcampensis, A. barnardi* and *A. mahe* are defined by two synapomorphies, one of which, is homoplastic, the relative length of antenna 1 and 2; and the other unequivocal, the presence of a bifid process on the carpal lobe of gnathopod 2.

Node G: the *aldabra–nedcampensis* clade.—These sister species are defined by a single derived character state.

Character 40: morphology of gnathopod 1.—These species share the geniculate condition of gnathopod 1 (state 1).

Node H: the *barnardi–mahe* clade.—These two species are also defined by a single apomorphic character state.

Character 28: proximal margin of carpus, gnathopod 2.—These two taxa have a distinct serrate ridge along the proximal insertion of the carpus (state 1).

Nodes I and J.—These nodes are supported by a single homoplastic character each indicating that they may not be reliable indicators of relationships. Further analysis of material will allow character relationships to be more thoroughly investigated.

Node K: Pacific Plate clade.—The taxa within this clade are supported by six characters, two of which are homoplastic and four unequivocal. While they are similar in gross morphology, they are readily distinguished by a variety of features, including variations in the broad ventral keel, coxal morphology and condition of the inner plate of the maxilliped. Only unequivocal characters are presented.

Character 7: inner plates of the maxilliped.—Inner plates entire, occasionally apically emarginate or with slight projections (state 4).

Character 16: carpal lobe of gnathopod 2.—All taxa have carpal lobes that are straight, thickened and blunt at the base (state 1).

Character 19: general morphology of gnathopod 2.—All species have a Type III second gnathopod, with a quadrate propodus, 2.5X length versus width, the long blunt carpus and straight dactyl extending one-half the length of the palm (state 2).

Character 37: apical ornamentation of inner plate, maxilliped.—All three species have an unusual condition of the inner plate, with the apical margins being slightly to sharply produced (state 1). In *A. bazimut* and *A. kateluensis* this condition was originally interpreted as the inner plates being cleft. My phylogenetic hypothesis supports the condition of projections extending from apically rounded margins, rather than representing a cleft condition. Additional material from other locations will elucidate the full range of traits for this group.

Node L: the presence of a sharp ventral keel (character 6, state 0) and a propodus of gnathopod 2 with variable ratio of teeth and cusps defining the palm (character 20, state 2) support this node. Both characters are homoplastic and thus provide only equivocal support.

Node M: the *excalibur* clade.—This branch is supported by five apomorphies, four of which are unequivocal. The large size of the head (character 3, state 2), the elongate palp article 4 of the maxilliped (character 8, state 2) and the enlarged first antennal peduncular segment (character 11, state 1) provide strong synapomorphic support for this unusual group of taxa. The elongate palp article 4 of the maxilliped is used in feeding, and its unique morphology may indicate specialised feeding adaptations. Additional investigations on feeding and host preference(s) for these taxa may explain the elongation of the fourth article and other morphological apomorphies.

Node N: *A. falarikia* and *A. papuaensis*.—These sister taxa are defined by seven apomorphies, two of which are homoplastic.

Character 2: relative length of antennae to body length.—The length of antenna 1 and 2 are less than one-half the body length (state 1). Since the antennae are used in feeding (Thomas, 1981; Thomas & Taylor, 1981), the use of this character in strictly defining taxa may prove problematical as more species are described and additional ecological studies are undertaken.

Character 12: relative length of antenna 1 versus antenna 2.—This homoplastic apomorphy shows substantial variation among species and clades. Its use in supporting phylogenies is questionable.

Character 13: relative size of coxa 2 versus coxae 2–4.—The immensely enlarged second coxa (state2) is unequivocal for these two species. Because second coxae are involved in feeding of anamixids it is hypothesised that these taxa have undocumented feeding or host relationships that could account for the immense increase in size of this character.

Character 16: length of carpal lobe, gnathopod 2.—The shortened carpal lobe, less than one-half of the palm (state 0), is found elsewhere only in the outgroup. The use of this character in feeding activities may determine its ultimate morphology. The equivocal nature of this character precludes its use as a strong indication of phylogenetic relationships, however, its occurrence in other clades may aid in hypothesising feeding behaviour.

Character 19: morphology of gnathopod 2.—The Type IV second gnathopod, with a short carpus and an oblique palm with numerous teeth or serrations (state 4) is unequivocal for these species, occurring nowhere else within *Anamixis*.

Character 21: dactyl of gnathopod 2.—The apically bifid dactyl (state 4) is unequivocal for *A. falarikia* and *A. papuaensis*.

Character 27: ventral margin of coxa 2.—The sinuous margin and large cuspate processes of the second coxae in these species (state 2) is also unequivocal for these two species.

Node O: eastern Pacific–Caribbean clade.—This clade is defined by three homoplastic apomorphies. Two of these characters provide support for this clade.

Character 10: shape and ornamentation of gnathopod 1.—All members of this clade have either a terminal spine or setae at the apex of gnathopod 1, or are carpochelate, with moderate or no basal inflation of the propodus (state 2). The only other occurrence of this condition is in *A. mahe* from the Seychelles Islands.

Character 13: relative size of coxa 2.—The moderately enlarged second coxa (state 1) is unequivocal for this clade. The presence of this state in *A. tangaroa* and *N. dianthus* warrants further analysis and refinement. The amount of enlargement in *A. tangaroa* and *N. dianthus* is not equal to the enlargement to found in this clade.

Node P: Caribbean clade.—Three homoplastic apomorphies define this clade restricted to the Caribbean Sea.

Character 6: shape of ventral keel.—Character states vary in two of the three taxa of this clade, rendering it unreliable.

Character 20: ornamentation of propodus, gnathopod 2.—Members of this clade all have a rectolinear propodus with major teeth or excavations on the palmar margin (state 3). A convergent condition in *A. excalibur* is the only other occurrence of state 3.

Character 38: apical ornamentation of dactyl, gnathopod 1.—The presence of long, paired terminal setae uniquely define the three species of Caribbean anamixids.

Node Q.—*Anamixis cavatura* and *A. vanga* are sister taxa based on the anterior margin of coxa 2 which has small teeth or cusps (character 14, state 1). This character is equivocal and additional character support at this node is needed for further resolution of relationships.

Biogeography

Distribution patterns resulting from the cladistic analyses can be explained in part by: 1, geological history, especially interactions at plate boundary margins; 2, effects of sea-level change and 3, effects of depressed sea-surface temperatures due to upwelling.

Geological activity and events at the margins of plates (e.g., docking of allochthonous terranes, volcanic uplift, coalescence of island arcs into composite terranes) may help explain the composite nature of some distribution patterns. Scenarios detailing composite faunas and how they may have accumulated have been put forth by Pandolfi (1992). For the purposes of this discussion, composite areas are defined as those areas where faunal composition appears to bridge wide geographic gaps, and documented population structure is composed of taxa with diverse geographic and phylogenetic affinities.

Glacial effects of sea-level change could cause widespread populations to be isolated thus making them more susceptible to genetic drift and possibly modify habitat and niche requirements. Maximum effects of this process would be in the intricate island coastlines of the Indo-Malayan region, an area from which comprehensive amphipod collections are almost totally lacking.

Depression of sea-surface-temperature would eliminate and fragment widespread populations of tropical amphipods, however, the data are insufficient to speculate about the historical effects of temperature on amphipod populations. One apparent anomaly in amphipod distribution related to water temperature is the occurrence of *A. tangaroa* in waters of the Bass Strait off southern Australia. Collected in cool deep waters (10°C; 60–82 m) *A. tangaroa* could be a disjunct relict of tropical transgressions into the higher latitudes. The cleft inner plats of the maxilliped of *A. tangaroa* clearly link it to the plesiomorphic genus *Nepanamixis*. Whether the occurrence of this species is atypical, or represents a common relict pathway (Newman, 1991) in species once more widespread during periods of tropical expansions remains to be addressed.

Nepanamixis

Of the four species in this clade, two, *Nepanamixis torreanus* from the Galapagos and *N. vectoris* from Panama are sister taxa. Current distributions probably resulted from rifting of the Nazca and Cocos Plates from the South American Plate which would have separated and split ancestral populations to the west. *Nepanamixis torreanus* retains the plesiomorphic condition of the inner plates and outer lobes of the maxilliped, while *N. vectoris* exhibits the more derived condition. The remaining two taxa *N. grossimana* and *N. dianthus*, present a widely disjunct distribution from Mauritius (Indian Ocean) to Belize (Caribbean Sea). I can provide no hypothesis for this distribution pattern. Additional sampling of reef sites, especially along plate boundary margins may produce additional species of *Nepanamixis*. Juvenile morphologies that differ drastically from other anamixid juveniles are known only from *N. dianthus* from Belize. Information on the juvenile morphologies of the remaining species of *Nepanamixis* is lacking, but efforts to document juvenile morphologies will further elucidate relationships within this clade. Commensal habitats (if any) and ecological niches are also unknown for all species of *Nepanamixis*. Any information regarding

the ecology of *Nepanamixis* will undoubtedly provide further insight regarding their habitat requirements.

Within *Anamixis* there are several recognisable distribution patterns in the Central and South Pacific (Node K), Eastern Pacific/Western Caribbean (Node O), Indian Ocean (Nodes G and I) and the South Pacific (Node M).

Three species, *A. bazimut, A. kateluensis* and *A. moana*, are widely distributed on the Pacific Plate and immediate margins to the south (Node K). *Anamixis moana* is known only from the Hawaiian islands and the emarginate inner plate of the maxilliped is apparently plesiomorphic. *Anamixis kateluensis* from the Caroline Islands, and *A. bazimut* from northern Papua New Guinea and the northern end of the Great Barrier Reef, Australia, both have apical projections in the inner plate of the maxilliped, apparently a derived condition.

Widespread distribution of a group suspected of having limited dispersal capabilities can be explained only by a reliction scenario (Newman, 1991). One plausible explanation would be the reliction and speciation of a previously widespread ancestral species. The resultant distribution pattern would be a series of closely related species with consistent morphological features and widespread distributions. Scenarios involving active dispersal of host and commensal do not appear plausible at this time.

Four species comprise the Indian Ocean component, *A. stebbingi* from the northern Indian Ocean, *A. aldabra* and *A. mahe* from the Seychelles and *A. nedcampensis*, from Western Australia. The two clades with Indian Ocean distributions, *A. aldabra* from Aldabra Atoll and *A. nedcampensis* from Ningaloo Reef, Western Australia (Node G); and *A. barnardi* from the littoral of South India and *A. mahe* from Mahe Island, Seychelles (Node H) are supported by equivocal characters. Node G is defined by the presence of a geniculate gnathopod 1, while Node H is defined by a denticulate carpal margin near the insertion of the propodus. A possible explanation for Indian Ocean distribution patterns was presented by Springer (1988). Essentially, the northward movement of the Indian subcontinent through the region divided ancestral components into two portions: western Indian Ocean and eastern Indian Ocean-Pacific Ocean. While there are eastern and western components to the distribution patterns, detailed scenarios that might account for this are as yet undeveloped.

Three species that share unusual character morphologies are distributed in the South Pacific, *A. papuaensis* from the south coast of Papua New Guinea, *A. falarikia* from the Caroline Islands and *A. excalibur* from the north coast of Papua New Guinea. Distributions in this group are more confined than the previous group of Pacific Plate species (Node K), with two of the species occurring at the north edge of the Australian Plate. *Anamixis papuaensis* and *A. falarikia* are sister species based on five unequivocal apomorphies (Node N), while *A. excalibur* is a sister taxa to the other two (Node M). Character support for this clade is strong with four unequivocal apomorphies. While species in this clade share distinct character states, there is considerable variation in morphology within this group. *Anamixis papuaensis* has a recurved medial process on the propodus, a derived condition not found anywhere else in the Amphipoda. Natural history studies to document host relationships and feeding behaviour may explain how these morphologies are used by the amphipods.

Four species comprise the eastern Pacific-Caribbean clade, *A. pacifica* from southern California and *A. hanseni, A. cavatura* and *A. vanga* from the Caribbean. These species have either a terminal spine or setal ornamentation on the apices of gnathopod 1. Thomas and co-workers have conducted extensive studies on *A. vanga* and *A. cavatura* describing feeding behaviour and biology in addition to documenting juvenile morphologies in these two species (Thomas, 1979, 1981; Thomas & Taylor, 1981; Thomas & Barnard, 1983). *Anamixis vanga* and *A. cavatura* are sister taxa, found throughout the central Caribbean and into the Carolinas. They overlap in range distributions but are separated by niche preferences, *A. cavatura* preferring small asconoid and colonial ascidians in relatively shallow depths (1–5 m), while *A. vanga* prefers larger solitary ascidians and occurs to deeper waters (2–20 m). Barnard (1955) listed "ascidians" as the host for *A. pacifica*. *Anamixis pacifica* was probably separated from its Caribbean counterparts by geological processes related to the formation of the Central American isthmus about three million years ago (Woodring, 1966).

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Amphipoda from the South Pacific: Western Samoa

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ABSTRACT. Forty species in twelve families of gammaridean Amphipoda are recorded from Upolu Island, Western Samoa. Three species are new to science, *Rostrogitanopsis cuculla* n.sp., *Maeracoota tridentata* n.sp. and *Ischyrocerus apiensis* n.sp. and are described and figured. Twenty-seven of the thirty-five species known from outside Samoa, are widespread. Eight species have limited extrinsic distributions, two being shared with Papua New Guinea, two with Fiji and Tonga, two with Kosrae (Micronesia) one with the Gambier archipelago and one with Moorea, Tonga and Fiji.

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Collections of gammaridean Amphipoda were made by the writer in 1979, at Upolu Island, Western Samoa, in 0–1.5 m and are reported on here. Forty species were collected of which three, *Rostrogitanopsis cuculla, Maeracoota tridentata* and *Ischyrocerus apiensis* are new to science. In addition, two new species have already been described from this material, *Cerapus oceanicus* Lowry (1985) and *Globosolembos tiafaui* Myers (1985a), neither of which has yet been recorded from outside Samoa.

The amphipod fauna of Western Samoa does not exhibit a close biogeographic affinity with that of any other particular Pacific island or archipelago. On the contrary, those species which are not widespread Pacific taxa are shared variously with islands to the east, west and north. Two species, *Bemlos tui* and *Gammaropsis planodentata* are known otherwise only from Papua New Guinea (Myers, 1995a), two species, *Elasmopus lapu* and *Lelehua malevua* are otherwise known only from Fiji (Myers, 1985b) and Tonga (Myers, 1986), two species, *Paradexamine tafunsaka* and *Elasmopus aduncus* are known otherwise only from Kosrae in Micronesia (Myers, 1995b) whilst one species, *Hyale dentifera* is currently known only from the Gambier Archipelago (Chevreux, 1907, 1908), and one species, *Parambasia nui* is known only from Moorea, Tonga and Fiji (Myers, 1985b, 1986, 1989). Thus Samoa has biogeographic links across much of the Pacific.

Figures and descriptions are here given of the three new species.

Type and voucher material is deposited in the collections of the Australian Museum, Sydney (AM). Station (stn) data and an annotated list of species records, are presented in Tables 1 and 2.

Table 1. Station (stn) data.

stn 1	Apia	Upolu Island	*Sargassum* in lagoon, 1 m, 15 September, 1979.
stn 2	Apia	Upolu Island	*Halimeda* from reef crest, 15 September, 1979.
stn 3	Apia	Upolu Island	*Turbinaria* from reef crest, 15 September, 1979.
stn 4	Apia	Upolu Island	*Halimeda* from reef front, <1 m, 15 September, 1979.
stn 5	Apia	Upolu Island	coral rubble in lagoon, 1 m, 15 September, 1979.
stn 6	Apia	Upolu Island	*Halimeda* in lagoon, 1 m, 15 September, 1979.
stn 7	Apia	Upolu Island	*Halodule* in lagoon. <1 m, 15 September, 1979.
stn 8	Matautu	Upolu Island	matted red algal turf in lagoon, 1 m, 16 September, 1979.
stn 9	Matautu	Upolu Island	foliose red alga in lagoon, 1 m, 16 September, 1979.
stn 10	Matautu	Upolu Island	coral rubble in lagoon, 1 m, 16 September, 1979.
stn 11	Matautu	Upolu Island	*Halimeda* in lagoon, 1 m, 16 September, 1979.
stn 12	Luatuanuu	Upolu Island	turf-like green alga on reef crest, 17 September, 1979.
stn 13	Luatuanuu	Upolu Island	*Halimeda* from reef crest, 17 September, 1979.
stn 14	Luatuanuu	Upolu Island	*Halodule* in lagoon, 1 m, 17 September, 1979.
stn 15	Luatuanuu	Upolu Island	coral rubble in lagoon, 1 m, 17 September, 1979.
stn 16	Luatuanuu	Upolu Island	*Amphiroa* in lagoon, 1 m, 17 September, 1979.
stn 17	Luatuanuu	Upolu Island	foliose red alga in lagoon, 1 m, 17 September, 1979.
stn 18	Luatuanuu	Upolu Island	*Sargassum* and *Turbinaria* in lagoon, 1 m, 17 September, 1979.
stn 19	Luatuanuu	Upolu Island	*Sargassum* and *Padina* in lagoon, 1 m, 17 September, 1979.

Abbreviations used in figures. **A1**, antenna 1; **d**, dorsal; **Ep1–3**, epimera 1–3; **G1–G2**, gnathopod 1–2; **ip**, inner plate; **Md**, mandible; **Mx1**, maxilla 1; **Mxp**, maxilliped; **p**, palp; **P3d–P7d**, dactylus of pereopods 3–7; **P3–7**, pereopods 3–7; **T**, telson; **U1–3**, uropods 1–3; **Us 1**, urosome segment 1.

Amphilochidae

Rostrogitanopsis Karaman

Rostrogitanopsis cuculla n.sp.

Figs 1, 2

Type material examined. HOLOTYPE ?male, 1.6 mm, AM P49550; PARATYPE male (dissected), AM P49551; Matautu, Upolu Island, matted red algal turf in lagoon, 1 m, A.A. Myers, 16.ix.79, stn 8.

Diagnosis. Male length 1.6 mm. Head produced into massive visor-like rostrum longer than combined length of first four pereon segments, lateral cephalic margin angular and sinuous, eye large, round, composed of numerous small ommatidea. Antenna 1 short, peduncular article 1 the longest, peduncular articles 2 and 3 subequal, flagellum with 4 articles bearing aesthetascs, accessory flagellum absent. Antenna 2 longer than antenna 1, more slender and with peduncular articles 4 and 5 subequal, flagellum with 5 articles. Mandible molar large, triturative, palp three articulate, articles in the basi-distal ratios 1:2:3, article 3 falcate. Maxilla 1 inner plate with a single terminal seta. Maxilliped palp article 3 subchelate. Gnathopod 1 coxa small, almost completely hidden beneath coxa 2, carpus and propodus small, slender, carpus two-thirds length of propodus, produced at posterodistal margin and bearing stiff setae. Gnathopod 2 coxa very large, subovoid, carpus and propodus small, slender, carpus and propodus subequal in length, carpus produced at posterodistal margin and bearing stiff, spine-like setae, dactylus with long terminal spine-like seta. Pereopods 3–4 slender, dactylus about one half length of propodus. Coxa 4 very large, excavate on posteroproximal margin. Pereopods 5–7 basis with large convex flange on posterior margin. Epimera 1–2 subtriangular, epimeron 3 subquadrate. Uropod 1 inner ramus a little longer than peduncle, outer ramus a little shorter than inner, both rami with a few marginal setae. Uropod 2 inner ramus markedly longer than peduncle, outer ramus a little over half length of inner, both rami with several marginal setae. Uropod 3 inner ramus two-thirds length of peduncle, outer ramus a little shorter than inner ramus, rami margins weakly setiferous and with a short distal spine-seta and fine seta. Telson elongate-triangular, apically tridentate.

Etymology. From the Latin *cucullus* meaning a hood, referring to the hood-shaped rostrum.

Remarks. Present material is undoubtedly very close to *Rostrogitanopsis mariae* (Griffiths) a species known only from the holotype collected in southern Moçambique (Griffiths, 1973) and a possible second specimen from Madagascar (Ledoyer, 1982). Ledoyer (1982) questioned whether his specimen was conspecific with the Moçambique specimen due to differences in size (Moçambique—7 mm, Madagascar—1.5 mm) the gnathopod setation, the shape of epimeron 3, and of the pereopod 5–7 bases. The present material is comparable in size with the Malagasy material but has a more strongly developed rostrum (longer than combined length of first four pereon segments, and nearly one quarter of body length) than either that species (one fifth body

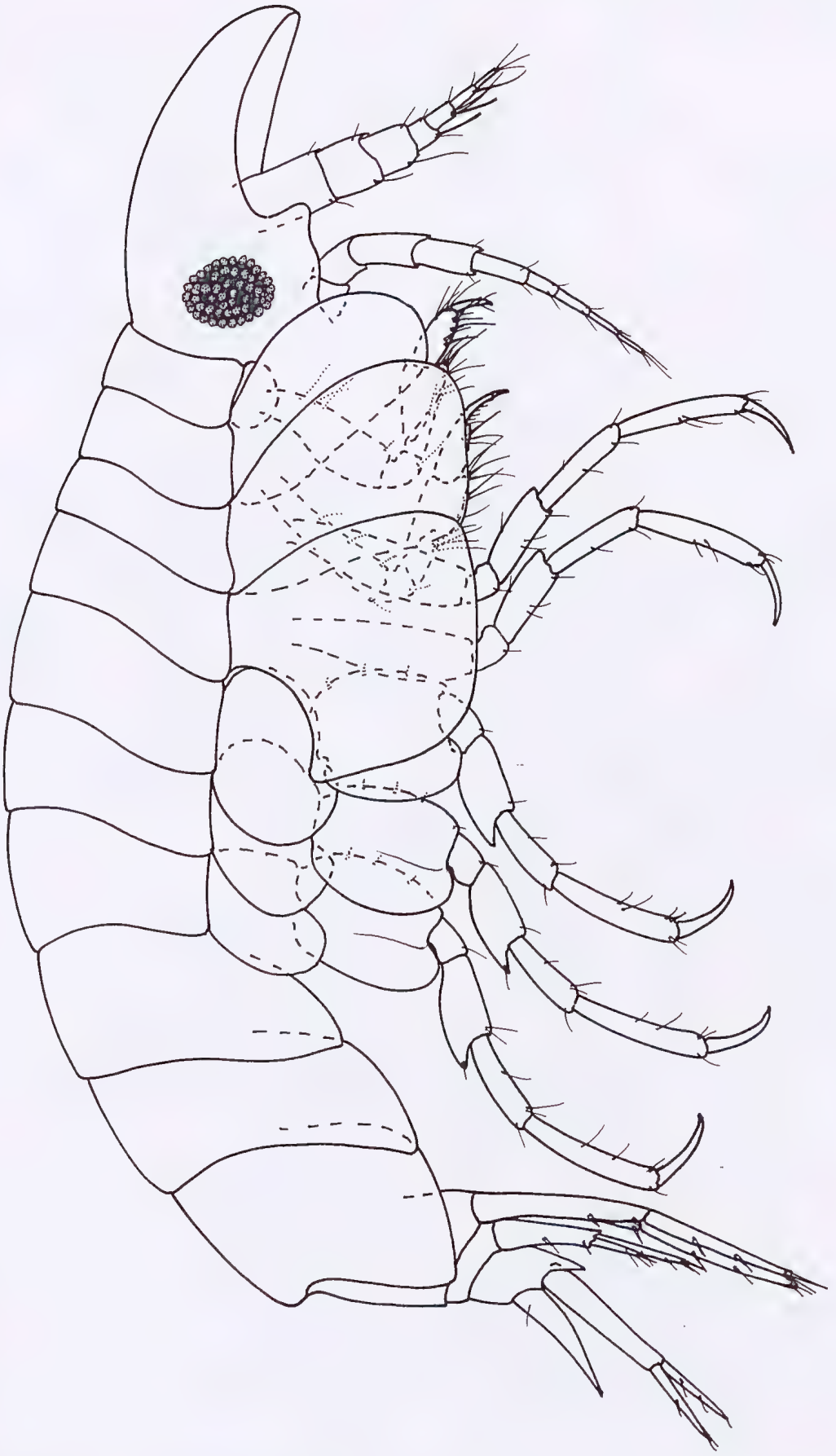

Fig. 1. *Rostrogitanopsis cuculla* n.sp. Paratype male, 1.6 mm, Matautu, Upolu Island, Western Samoa.

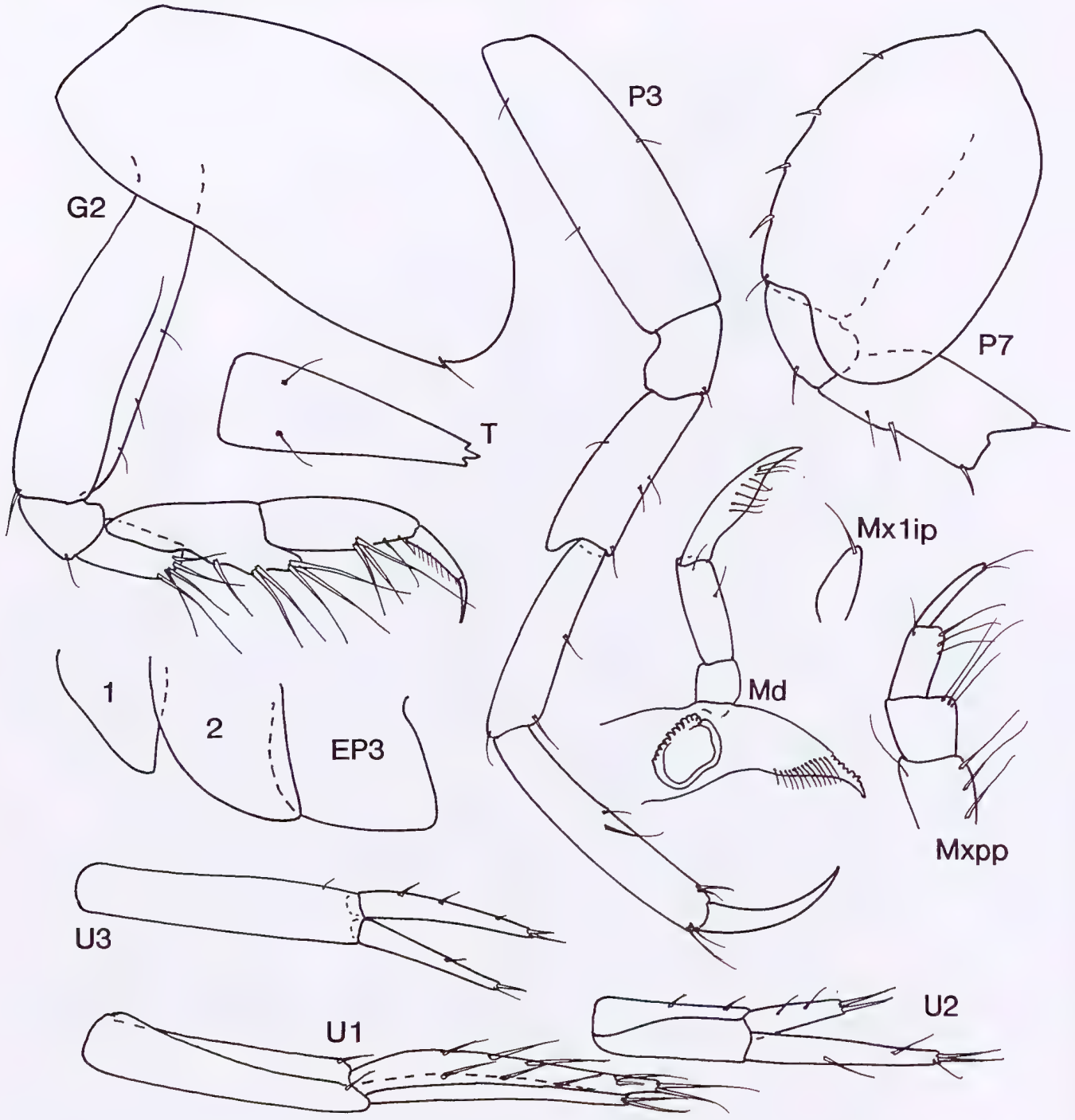

Fig. 2. *Rostrogitanopsis cuculla* n.sp. Paratype male, 1.6 mm, Matautu, Upolu Island, Western Samoa.

length) or the Moçambique specimen (shorter than combined length of first three pereon segments). Antenna 1 and 2 are subequal in both Moçambique and Malagasy material, but antenna 2 is distinctly longer than antenna 1 in present material. Like the Malagasy material, present material has strong setae on the gnathopod 1–2 carpus and subovoid pereopod 5–7 basis. On the other hand, epimeron 3 is similar to that described by Griffiths (1973) from Moçambique. According to Griffiths (1973), Moçambique material has the outer ramus of uropods 1–3 marginally shorter than the inner. According to the figures of Ledoyer (1982) of Malagasy material, the uropod 1 outer ramus is less than half the length of the inner ramus and the uropod 2 outer ramus is about two-thirds the length of the inner ramus. In present material, the outer ramus of uropod 1 is only a little shorter than the inner ramus and the outer ramus of uropod 2 is a little over half the length of the inner ramus. In present material the mandibular palp is similar to that of Moçambique material, article 2 being relatively short, and article 3 falciform. The mandibular palp of the Malagasy material on the other hand, has an

elongate and slender article 2 and a slender, straight article 3. A feature not figured or described by either Griffiths or Ledoyer, is the presence of an elongate "nail" on the end of the dactylus of the gnathopod 2.

The poorly known morphology of *R. mariae* from Moçambique and of the ?*R. mariae* from Madagascar makes it dificult to determine whether the present material is synonymous with either. Since it does not agree fully with either species and demonstrates a unique character (gnathopod 2 dactylus) it seems sensible to allocate present material to a new species. Examination of more abundant material from southern Africa will be necessary to shed further light on relationships.

Melitidae

Maeracoota n.gen.

Diagnosis. Head lacking an anterocephalic notch. Mandible palp 3-articulate, article 2 longer than article 1, article 3 almost as long as article 2. Maxilla 1 inner plate well-developed with two terminal setae. Gnathopod 1 coxa with acute anterodistal margin, carpus subdistal anterior margin with indentation, inner face with extensive spine rows. Gnathopod 2 massively developed, carpus short, cup-shaped, propodus broadest distally. Pereopods 3–4 dactylus distally bifid, pereopods 5–7 basis with posterior margin toothed, dactylus distally trifid. Epimera 1–2 with single acute posterodistal tooth. Epimeron 3 posterior margin scalloped, Urosomite 1 with 3 dorsal teeth. Telson fully divided, each side deeply notched.

Type species. *Maeracoota tridentata* n.sp. monotypic.

Remarks. This genus agrees with *Maera sensu stricto* in lacking a head notch (note that *Maera sensu lato* includes species with a head notch, e.g., *M. octodens*) and in having a notched gnathopod 1 carpus (also missing in some *Maera sensu lato*, e.g., *M. hamigera*), but that genus never has teeth on either the pleonites or urosomites. It is similar to *Ceradocus* but that genus has teeth on pleonites 1–3 as well as on urosomites 1–2, a very short mandible palp article 3 and cephalic notch. In bearing teeth on urosomite 4, it resembles *Mallacoota*, but that genus has two teeth only i.e. lacks a medial tooth and also has a notched cephalic lobe.

In general this genus appears to be closest to *Maera* with which it may ultimately be synonymised. However, the genera *Maera, Mallacoota, Hoho, Parelasmopus, Ifalukia, Ceradocus* and perhaps *Elasmopus* are probably polyphyletic as currently constituted. *Mallacoota* represents the development of a toothed urosomite from maerids with a head notch while *Maeracoota* represents the development of a toothed urosomite from maerids lacking a head notch. It would seem, therefore, appropriate to recognise this genus as distinct until a thorough revision of the above complex can be carried out.

Etymology. Constructed from the names of the genera *Maera* and *Mallacoota*.

Maeracoota tridentata n.sp.

Figs 3, 4

Type material examined. HOLOTYPE male, 5.0 mm (unique), AM P49552; Luatuannuu, Upolu Island, *Halodule* in lagoon, 1 m, A.A. Myers, 17.ix.79, stn 14.

Diagnosis. Male length 5.0 mm. Head with ocular lobes rounded-quadrate, and lacking a subocular cephalic notch. Antenna 1 peduncular article 1 with well-developed posterodistal acute tooth, peduncular articles in the length ratios 7:8:2, accessory flagellum well-developed with 8 long articles and one rudimentary terminal article, primary flagellum broken with 16+ articles. Antenna 2 slender, peduncular article 3 with well-developed posterodistal acute tooth, peduncular articles 4 and 5 in the ratio 4:3, flagellum shorter than peduncular article 5 with 6 articles, the terminal article rudimentary. Mandible palp with three articles, in the basi-distal ratios 3:9:8, article 3 slender, almost parallel-sided, with 3 long distal setae and with three evenly spaced long setae on the posterior margin. Maxilla 1 inner plate elongate with two unequal distal setae and one subdistal seta. Gnathopod1 coxa anterodistal corner acute, carpus anterodistal margin with indentation, inner face with rows of short, stout spine-setae, propodus shorter than carpus, palm oblique, evenly continuous with posterior margin but defined by a cluster of three spine-setae. Gnathopod 2 massive, merus posterodistal margin acutely produced, carpus short, cup-shaped, propodus nearly four times length of carpus, broadest distally, palm oblique, irregularly scalloped, defined by strong, short, triangular tooth, dactylus large, falcate, fittring palm. Pereopods 3–4 small, slender, dactylus less than half length of propodus, distally bifid. Pereopods 5–7 basis posterior margin saw-toothed, dactylus distally trifid. Epimera 1–2 with posterodistal margin swept out into an acute tooth. Epimeron 3 posterior margin scalloped with 8 acute teeth. Urosomite 1 with a medial tooth and two dorsolateral teeth. Uropod 1 inner ramus a little longer than outer and three-quarters length of peduncle. Uropod 2 inner ramus longer than outer and subequal with peduncle. Uropod 3 missing. Telson divided to the base, each half with two strong acute teeth and two pairs of unequal distal setae.

Female unknown.

Etymology. From the latin *tri* = three and *dens* = tooth, referring to the three teeth on the urosomite.

Remarks. The complex dactyls of pereopods 3–7 are very similar in structure to those of *Maera serrata* Schellenberg, *M. inaequipes* (Costa) and *M. kaiulani* Barnard and are also found in a more rudimentary form in *M. quadrimana* and *M. pacifica*.

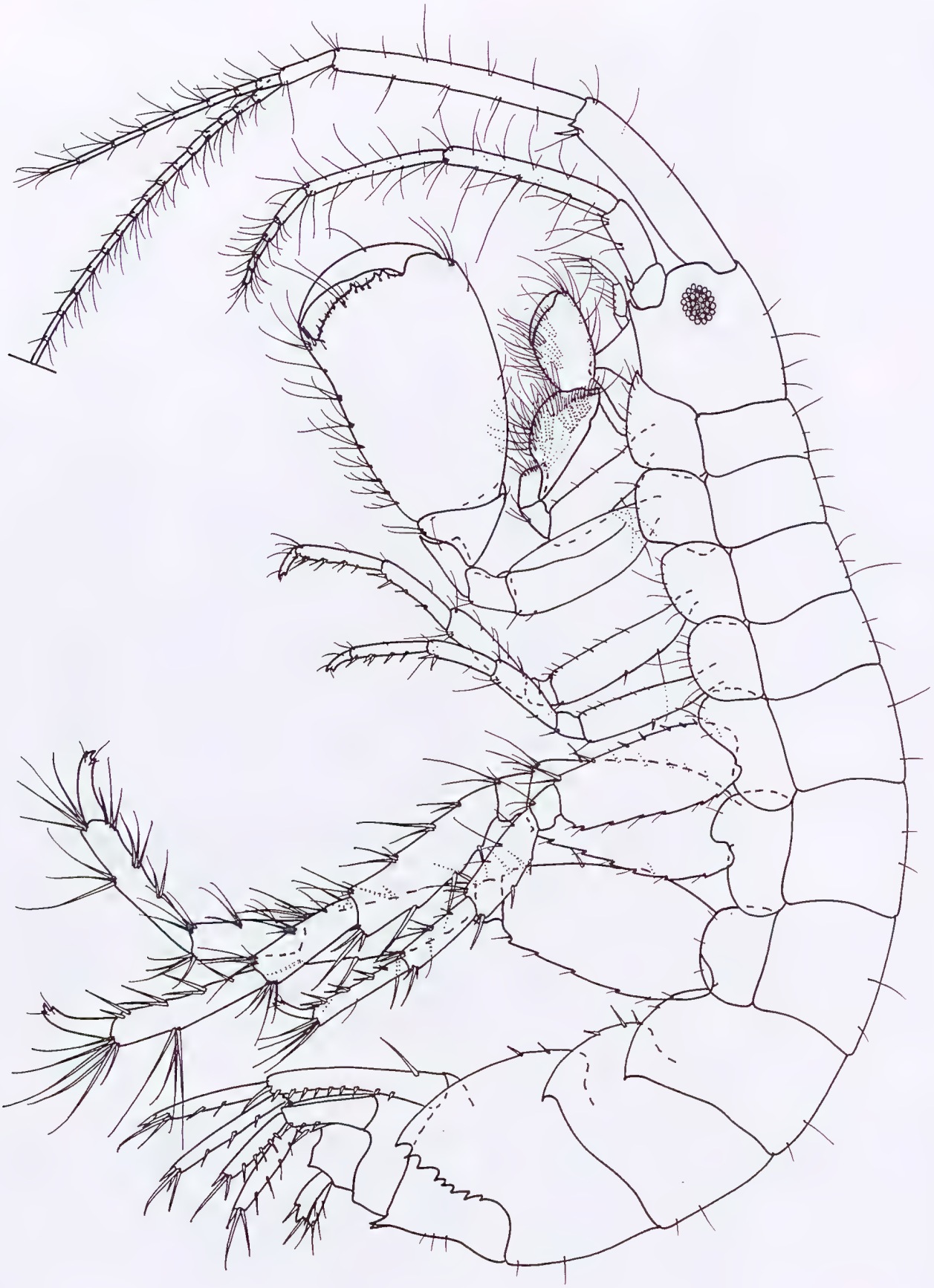

Fig. 3. *Maeracoota tridentata* n.gen. et sp. Holotype male, 5.0 mm, Luatuanuu, Upolu Island, Western Samoa.

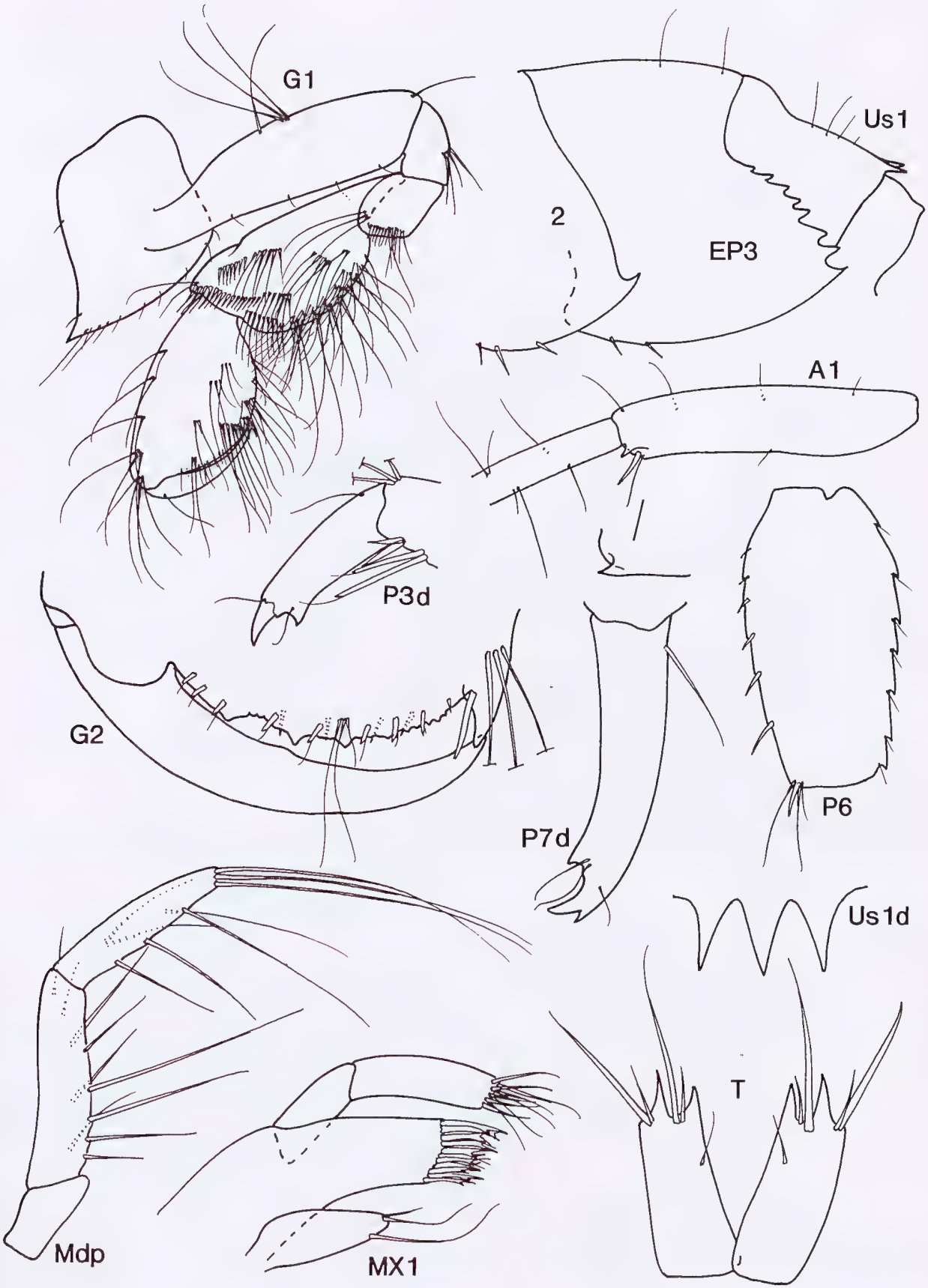

Fig. 4. *Maeracoota tridentata* n.gen. et sp. Holotype male, 5.0 mm, Luatuanuu, Upolu Island, Western Samoa.

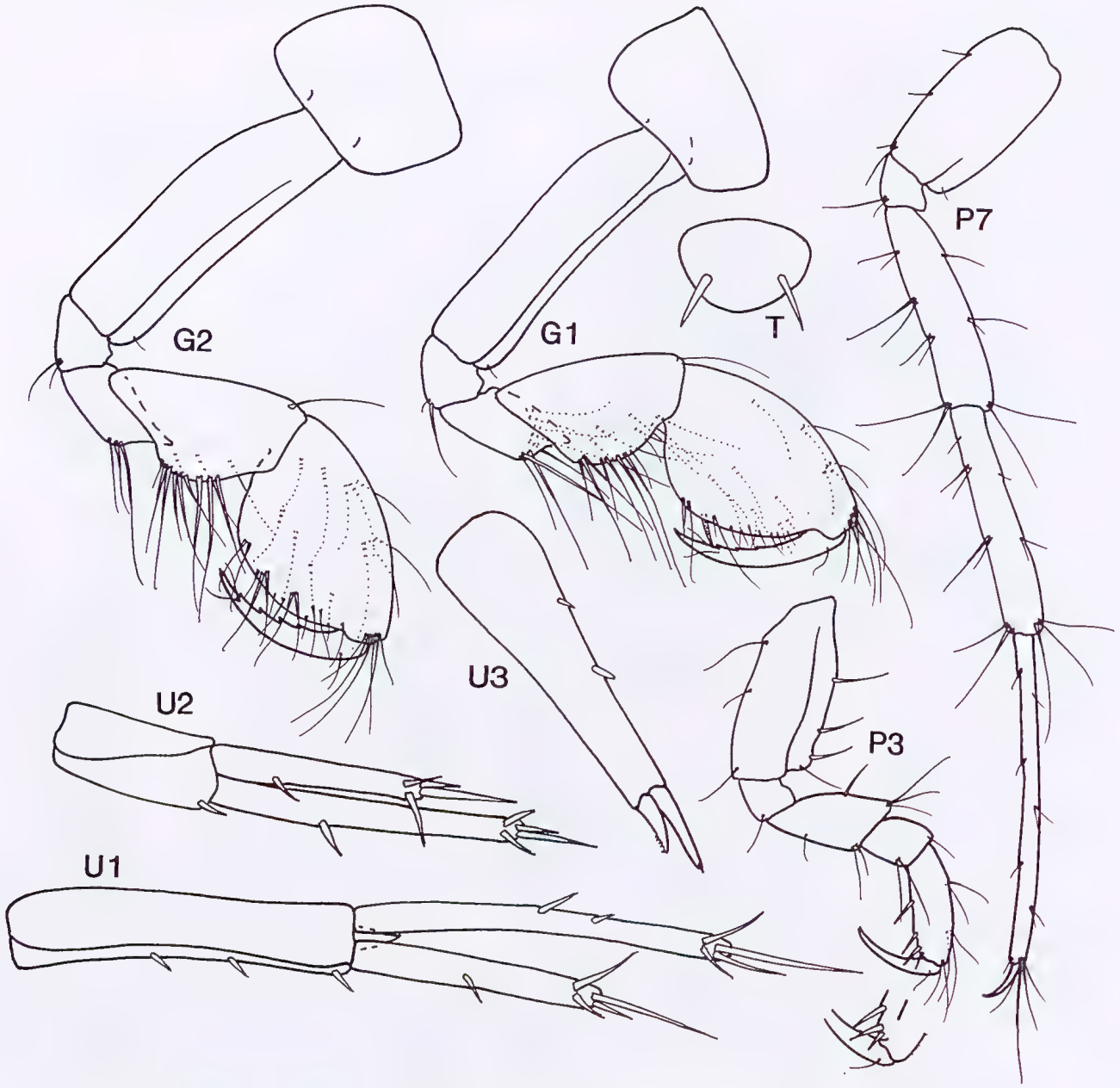

Fig. 5. *Ischyrocerus apiensis* n.sp. Paratype female, 1.2 mm, Apia, Upolu Island, Western Samoa.

Ischyroceridae

***Ischyrocerus* Kroyër**

***Ischyrocerus apiensis* n.sp.**

Fig. 5

Type material examined. HOLOTYPE female, 1.2 mm, AM P49553; PARATYPE female, 1.2 mm, AM P49554; Apia, Upolu Island, Western Samoa, coral rubble in lagoon, 1 m, A.A. Myers, 15.ix.79, stn 5.

Diagnosis. Length 1.2 mm. Lateral cephalic lobes moderately produced, rounded, eyes large. Antennae unknown. Mouthparts like those of *Jassa lilipuna* Barnard (1970). Gnathopod 1 coxa narrow, basis elongate, carpus subtriangular, propodus a little longer than carpus, posterior margin and palm continuous, evenly rounded, dactylus elongate and slender. Gnathopod 2 coxa broader but otherwise not different from gnathopod 1. pereopods 3–4 stout, basis expanded with anterior irregular flange bearing 4 long recurved setae, propodus with a strong locking spine and two further strong marginal spines, dactylus about three quarters length of propodus. Pereopods 5–6 unknown. Pereopod 7 basis expanded, flange on posterior margin smooth, propodus very elongate, one and one half times length of carpus. Epimera 1–3 rounded. Uropod 1 peduncle with short inter-ramal tooth, inner ramus longer than outer and longer han peduncle. Uropod 2 peduncle lacking an inter-ramal tooth, inner ramus longer than outer and

almost twice length of peduncle. Uropod 3 peduncle elongate-pyriform, inner ramus less than one third length of peduncle and with a single, short, terminl spine, outer ramus two thirds length of inner ramus, with about four reverted terminal cusps. Telson distally rounded, with a pair of very stout dorsal spines.

Ovigerous female with 4 eggs.

Male unknown.

Etymology. From the collection locality.

Remarks. This species belongs to an Indo-Pacific tropical complex of diminutive taxa currently placed in *Ischyrocerus* or *Jassa* but actually requiring a new genus (see Myers, 1995a). The species described to date which belong to this unnamed genus are: *Jassa lilipuna*, from Hawaii, *J. socia* Myers (1989), from the Society Islands, *Ischyrocerus kapu* (Barnard, 1970) and *I. oahu* Barnard (1970), from Hawaii and *I. parma* Myers (1995a) and *I. mediodens* Myers (1995a) from Papua New Guinea. I have refrained from erecting a new genus because this is being done elsewhere (see Conlan, 1990).

In having strong spines on the posterior margin of the propodus of pereopods 3–4, the present species resembles *I. mediodens* Myers and *I. oahu* Barnard. It differs, however, from both these two species and indeed from all described species of this complex, by the extremely elongate pereopod 7 propodus.

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Table 2. Annotated list of species recorded from Western Samoa. Number of male (M), female (F) and immatures (imm) recorded; see Table 2 for station data.

family	species	M	F	imm.	station
AMPHILOCHIDAE	*Amphilochus menehune* Barnard	–	3	–	3
	A. menehune	1	2	–	5
	A. menehune	2	5	–	8
	A. menehune	1	1	1	15
	A. menehune	–	1	–	16
	A. menehune	1	–	–	19
	Gitanopsis tai Myers	1	1	–	10
	Rostrogitanopsis cuculla n.sp.	2	–	–	8
AMPITHOIDAE	*Ampithoe kava* Myers	10	14	–	1
	A. kava	2	–	–	7
	A. ramondi Audouin	37	43	9	2
	A. ramondi	14	23	–	3
	A. ramondi	6	11	2	4
	A. ramondi	–	1	–	6
	A. ramondi	6	10	2	8
	A. ramondi	5	10	–	9
	Cymadusa brevidactyla (Chevreux)	7	16	3	8
	C. brevidactyla	–	2	2	10
	C. imbroglio Rabindranath	3	7	3	7
	C. imbroglio	3	3	1	9
	C. pilipes (Ledoyer)	8	7	3	3
	Paragrubia vorax Chevreux	1	–	–	8
	P. vorax	1	1	1	12
	Pleonexes kulafi Barnard	1	3	–	1
	P. kulafi	2	5	–	3
	P. kulafi	1	–	–	7
	P. kulafi	–	1	–	14
	P. kulafi	1	–	–	17
	P. kulafi	3	20	–	18
	P. kulafi	8	10	–	19
	P. kulafi	1	1	–	15
AORIDAE	*Bemlos aequimanus* (Schellenberg)	12	9	–	6
	B. aequimanus	2	3	–	7
	B. aequimanus	1	3	–	9
	B. aequimanus	1	3	–	11
	B. aequimanus	–	2	–	8
	B. aequimanus	1	1	–	17
	B. aequimanus	1	1	–	19
	B. aequimanus	1	–	–	14
	B. dentischium taparum (Myers)	4	4	5	8
	B. dentischium taparum	3	7	–	11
	B. tui Myers	1	1	–	10
	B. tui	–	1	–	4
	Globosolembos ovatus Myers	2	2	–	5
	G. ovatus	6	6	2	15
	G. ovatus	7	3	–	10
	G. tiafaui Myers	9	8	3	5
EUSIRIDAE	*Tethygeneia pacifica* (Schellenberg)	–	1	–	8
DEXAMINIDAE	*Paradexamine tafunsaka* Myers	–	1	–	1
	P. tafunsaka	–	3	–	5
	P. tafunsaka	–	2	–	15
	P. tafunsaka	–	2	–	11
	P. tafunsaka	–	2	–	8
	P. tafunsaka	1	3	–	10
	P. tafunsaka	–	1	–	9
HYALIDAE	*Hyale dentifera* Chevreux	1	1	1	8
	H. dentifera	1	–	–	14
	H. dentifera	1	2	–	15
	Lelehua malevua Myers	6	3	–	14
	L. malevua	44	30	3	12

Table 2. Continued.

family	species	M	F	imm.	station
	L. malevua	3	5	–	2
	L. malevua	1	–	–	10
ISAEIDAE	*Gammaropsis atlantica* Stebbing	1	–	–	5
	G. atlantica	–	1	–	9
	G. digitata (Schellenberg)	21	25	10	2
	G. digitata	11	10	1	3
	G. digitata	4	8	–	4
	G. digitata	2	3	–	5
	G. digitata	–	1	–	7
	G. digitata	18	19	3	8
	G. digitata	10	12	–	9
	G. digitata	6	6	–	11
	G. digitata	8	1	–	12
	G. digitata	11	7	–	14
	G. digitata	1	1	–	15
	G. digitata	5	5	–	16
	G. digitata	–	2	1	18
	G. planodentata Myers	1	4	–	5
	G. planodentata	–	2	–	9
	G. planodentata	1	1	–	10
ISCHYROCERIDAE	*Cerapus oceanicus* Lowry	14	12	3	5
	C. oceanicus	–	–	1	14
	Ischyrocerus apiensis n.sp.	–	2	–	5
LEUCOTHOIDAE	*Leucothoe hyhelia* Barnard	2	–	–	2
	Leucothoella banwarthi Schellenberg	1	1	–	2
LYSIANASSIDAE	*Parambasia nui* Myers	–	1	–	10
	Parawaldeckia lowryi Myers	–	7	2	2
	P. lowryi	–	1	–	11
	P. lowryi	–	1	–	15
MELITIDAE	*Elasmopus aduncus* Myers	15	10	–	14
	E. aduncus	9	7	–	15
	E. aduncus	2	4	–	17
	E. aduncus	1	–	–	4
	E. aduncus	33	60	4	2
	E. gracilis Schellenberg	1	4	1	14
	E. gracilis	1	3	1	7
	E. gracilis	1	1	–	9
	E. gracilis	2	7	–	11
	E. hooheno Barnard	2	2	–	5
	E. lapu Myers	22	30	3	8
	E. lapu	12	4	1	12
	E. lapu	1	–	1	10
	E. pseudaffinis Schellenberg	19	34	–	6
	Maera hamigera Haswell	1	–	–	8
	M. hamigera	1	–	–	10
	M. pacifica Schellenberg	–	1	–	4
	M. pacifica	–	1	–	8
	M. pacifica	3	4	–	2
	M. serrata Schellenberg	5	9	–	6
	M. serrata	1	–	–	11
	Maeracoota tridentata n.sp.	–	1	–	14
	Mallacoota insignis (Chevreux)	13	11	–	4
	M. insignis	11	13	–	14
	M. insignis	2	–	–	15
	M. insignis	11	12	–	8
	M. insignis	5	11	–	2
	M. insignis	–	1	–	9
	M. insignis	1	3	–	16
	M. insignis	11	10	–	12
	Parelasmopus suensis (Haswell)	1	–	–	9
STENOTHOIDAE	*Stenothoe* sp.	–	–	2	5

Erratum

Amendment to: Griffin, D.J.G., & H.E. Stoddart, 1995. Deep-water decapod Crustacea from eastern Australia: lobsters of the families Nephropidae, Palinuridae, Polychelidae and Scyllaridae. Records of the Australian Museum 47(3): 231–263.

Ms Diane Brown, formerly of the Crustacea Department of the Australian Museum, contributed substantially to early drafts of the above paper, recently published in the *Records of the Australian Museum*. We regret that Ms Brown's name was not included in the published acknowledgments of this paper and here gratefully acknowledge her contribution.

D.J.G.G. & H.E.S.

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A New Species of *Syscenus* Harger, 1880 (Crustacea: Isopoda: Aegidae) from Eastern Australia, With a Revised Diagnosis of the Genus

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ABSTRACT. *Syscenus springthorpei* n.sp. is described from a single specimen taken from the south-eastern Australian coast at a depth of about 500 m. This species is characterised by a sub-acute pleotelson apex, uropods that do not extend beyond the posterior margin of the pleotelson and a short antennal flagellum that does not extend beyond pereonite 3. A revised diagnosis of the genus and an annotated list of the known species is presented.

BRUCE, NIEL L., 1997. A new species of *Syscenus* Harger, 1880 (Crustacea: Isopoda: Aegidae) from eastern Australia, with a revised diagnosis of the genus. Records of the Australian Museum 49(2): 113–120.

The genus *Syscenus* is widely distributed throughout the world oceans. The species comprising this genus are usually known from single specimens from diverse localities. *Syscenus* has not previously been recorded from Australian waters and there exists only a single record from the Southwest Pacific: that of Monod (1973), which is considered of doubtful identity. The record of this genus brings the number of aegid genera known from Australian waters to four, only the Atlantic genus *Xenuraega* Tattersall, 1909 (Bruce 1993) and the pelagic genus *Barybrotes* Schiødte & Meinert, 1879 being absent. Brusca (1983) reviewed the history of the taxonomy of the family and Bruce (1993) provided a key to the known genera.

Abbreviations used: AM—Australian Museum, Sydney; BL—body length; PMS—plumose marginal setae; PS—plumose setae; ZMUC—Zoologisk Museum, University of Copenhagen, Denmark.

Taxonomy

Genus *Syscenus* Harger

Syscenus Harger, 1880: 387.–Sars, 1899: 66.–Richardson, 1905: 212.–Stebbing, 1924: 9.–Wahrberg, 1930: 24.–Nierstrasz & Schuurmans Steckhoven Jr., 1930: 77.–Schultz, 1969: 196.–Menzies & George, 1972: 12.–Kussakin, 1979: 269.

Harponyx Sars, 1882: 60 (type species *Harponyx pranizoides* Sars, 1882).

Rocinela.–Bovallius, 1885: 4 (not *Rocinela* Leach, 1818).

Syscénus.–Stephensen, 1948: 41.

Type species. *Syscenus infelix* Harger, 1880, by monotypy. Gender neuter.

Diagnosis. Body elongate, about 3 to 4 times as long as wide. Cephalon without eyes, anterior margin forming median point. Coxae present on pereonites 2–7, those of pereonites 4–7 shorter than respective segment, not posteriorly produced. Pleon abruptly narrower than pleon, about 30–40% BL; pleonites all visible, becoming progressively wider towards posterior, with free lateral margins; pleonites 3–5 lateral margins produced to form an acute point. Pleotelson large, as long or longer than pleon, usually with caudomedial point. Pleonal sternite present anterior to pleopod 1 peduncles.

Antennule peduncle 3-articulate, antenna peduncle 5-articulate; flagellae of both not extending to pleon.

Frontal lamina, clypeus and labrum present. Mandible with unicuspid incisor; molar process and spine row absent; palp 3-articulate. Maxillule slender, styliform, with 5 hooked, terminal spines; reduced medial lobe present. Maxilla lateral lobe present, with 3 recurved terminal spines. Maxilliped 4 articulate, article 3 with 2–3 recurved spines, article 4 with 1 recurved spine; endite absent.

Pereopods 1–3 robust; distal margins of ischium to merus with long simple setae; dactylus prehensile, strongly recurved, longer than propodus. Pereopods 4–7 becoming progressively longer; ischium to propodus provided with spines and abundant simple setae; dactylus shorter than propodus, weakly recurved.

Pleopods 1 and 2, both rami with PMS; pleopods 3–5 endopods with reduced setae (pleopod 3) or naked, distinctly smaller than exopods; coupling hooks present on peduncles of pleopods 1–5; pleopods not extending beyond pleotelson lateral margins. Uropods flat, lamellar; endopod longer than exopod.

Remarks. The genus is readily separated from all others of the family except *Xenuraega* by the pleon being abruptly narrower than the pereonite 7. *Syscenus* and *Xenuraega* are readily differentiated by *Syscenus* having a frontal lamina and lamellar uropods with both rami prominent, while *Xenuraega* lacks a frontal lamina and has a filamentous uropodal exopod and a stub-like endopod.

Several accounts illustrate the maxilliped as having only three articles (Harger 1883; Sars, 1899; Menzies & George, 1972; Monod, 1973; Nunomura, 1981). Examination of Atlantic specimens of *Syscenus infelix* (ZMUC CRU2073-2076) show that a small fourth maxilliped article (as illustrated here in Fig. 2G) is in fact present. The generic diagnosis given here is based on the type species and the new species described herein. The extent of character variation within the genus is not possible to assess as the remaining species are inadequately described.

Species of the genus have been recorded at depths between 146 and 3260 m.

Species included

Syscenus atlanticus Kononenko, 1988. This species has been recorded from a single North Atlantic location at a depth between 810–860 m. It is not possible to characterise this species against other congeneric species, although the original figures suggest that it differs from *Syscenus infelix* in having a broadly rounded pleotelson, and far longer antennal flagellae, supported by the examination of previously unreported material (ZMUC CRU2077).

Syscenus infelix Harger, 1880. The type species and the most widely recorded species of the genus. The type locality is "15 miles northeast of Cape Cod," northwestern Atlantic (Harger 1880). The species has been reported from depths between 146 and 1117 m; records are from the northeastern and northwestern North Atlantic (Richardson, 1905), Japan (Richardson, 1909) the Philippines (Richardson, 1910), New Caledonia (Monod, 1973) and South Africa (Stebbing, 1924). Given the differences noted between Japanese and Atlantic specimens, the condition of the Philippine specimen, and lack of detail in the early records, confirmation of all these localities is required.

Syscenus intermedius Richardson, 1910. Known only from the Philippines, Albatross Station 5301.

Syscenus latus Richardson, 1909. Known only from Japan, taken at a depth of 742 m, southwest of Koshika Island, c. 31°39'N 129°20–23'E.

Syscenus pacificus Nunomura, 1981. Known only from the East China Sea, 660–990 m. Nunomura (1981, p. 16) apparently believed that he was describing only the second species of the genus, overlooking the publications of Richardson (1909, 1910) and Menzies & George (1972). The illustrations of Nunomura (1981) show striking points of resemblance to *S. latus* from the same area and the validity of *S. pacificus* is open to question.

Syscenus peruanus Menzies & George, 1972. The species is based on a juvenile with eyes, taken from the Peru-Chile Trench at a depth of 3254–3260 m.

Syscenus springthorpei n.sp.

Figs 1–4

Type Material. HOLOTYPE: male (36 mm), east of Long Reef Point, Broken Bay, New South Wales, Australia, 33°41'S 151°55'E, 19 December 1985, 476–531 m, coll. R.T. Springthorpe on FRV *Kapala* (AM P37507).

Other species examined: 1 specimen each of *Syscenus atlanticus* (ZMUC CRU2077) and *Syscenus latus* (ZMUC CRU2079); 4 samples of Atlantic *Syscenus infelix* (ZMUC CRU2073-2076).

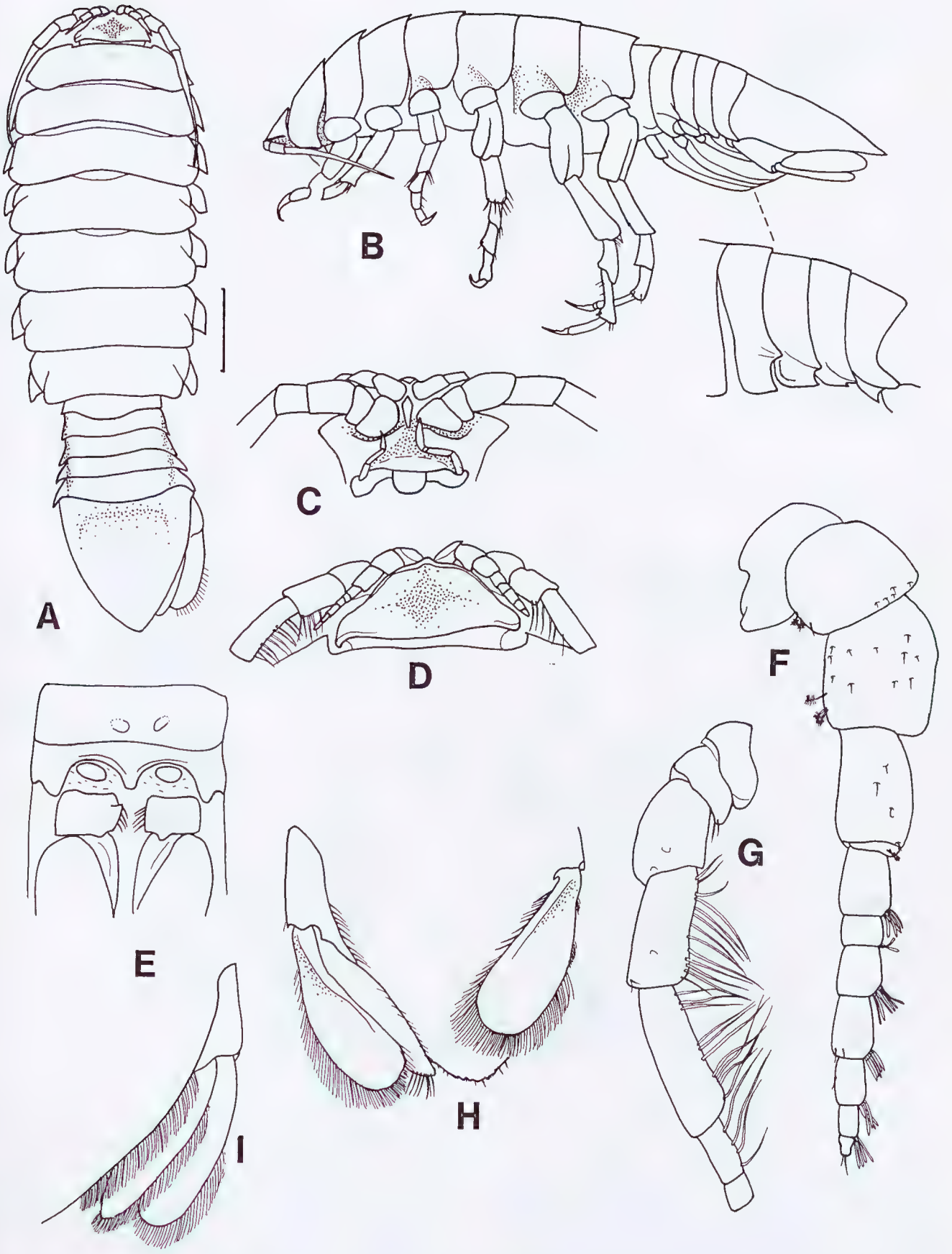

Fig. 1. *Syscenus springthorpei* n.sp., holotype. A, dorsal view; B, lateral view and pleon detail; C, frons; D, cephalon, dorsal view; E, sternite 7 showing penial openings and pleonal sternite; F, antennule; G, antenna peduncle; H, pleotelson and uropods, ventral view; I, uropods, in situ, dorsal view. Scale 5.0 mm.

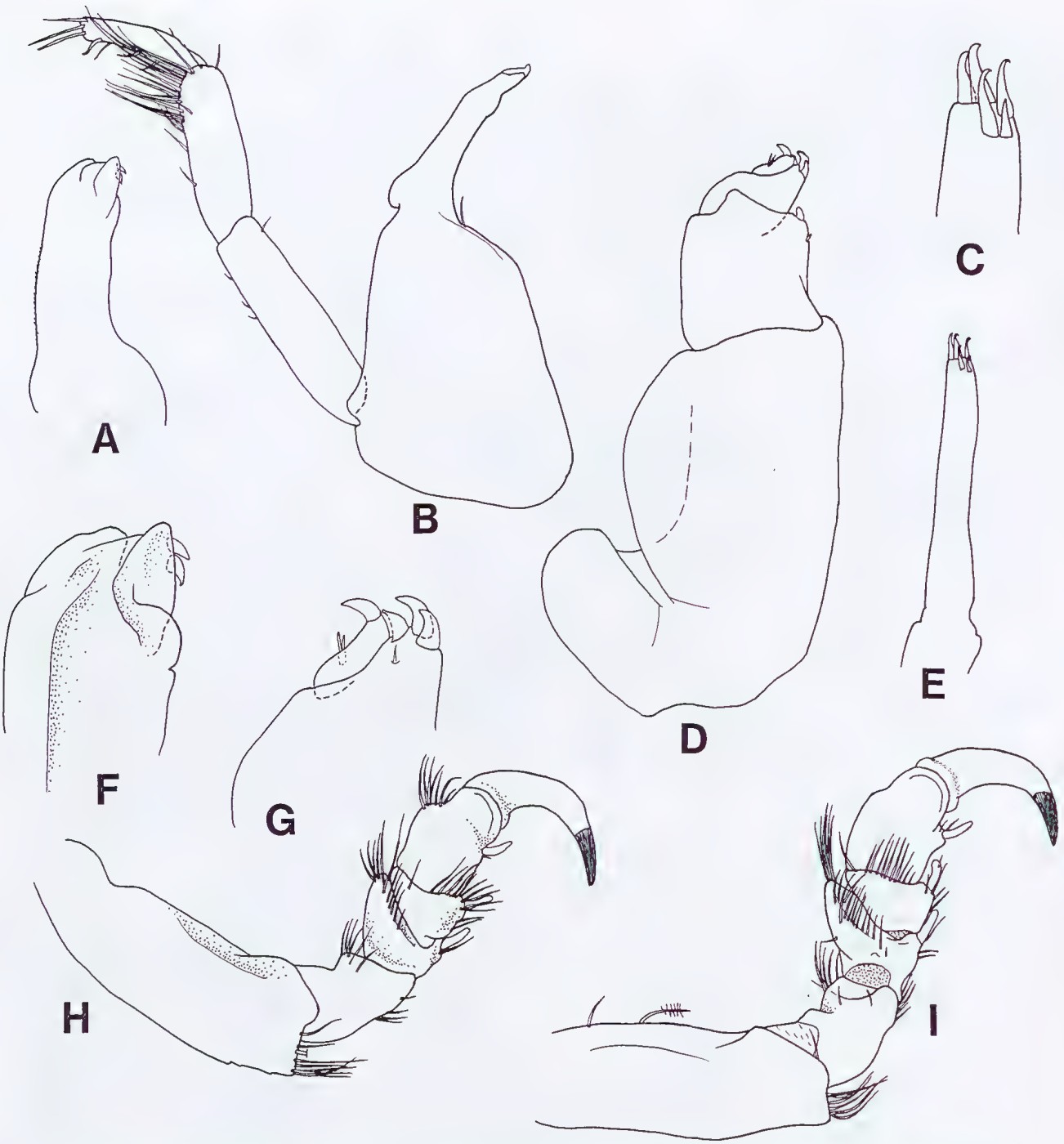

Fig. 2. *Syscenus springthorpei* n.sp., holotype. A, maxilla; B, mandible; C, maxillule apex; D, maxilliped; E, maxillule; F, maxilla apex; G, maxilliped palp, terminal articles; H, pereopod 1; I, pereopod 2.

Description of male holotype

Body: about 3 times as long as greatest width, dorsal surfaces smooth, unornamented; lateral margins subparallel; maximum width at pereonites 3–6. *Cephalon*: with small but distinct median rostral process; anterolateral margins sinuate; posterior margin forming distinct ridge, posterior to which is abruptly narrower ("neck-like" in appearance); eyes absent, ocular lobes weakly developed. *Pereonites*: 5 and 6 longest, subequal in length; pereonite 1<2=3<4<5=6>7; posteroventral angle of pereonite 1 forming acute point; coxae not extending beyond posterior of segment, those of pereonites 2–3 posteriorly rounded; pereonites 4–6 truncate; pereonite 7 posteriorly subacute. *Pleon* about 16% BL, markedly narrower than pereon, anteriorly 0.4 times as wide as maximum pereonal width; all pleonites visible with free lateral margins; pleonites 4 and 5 wider than 1–3; posterolateral angles of pleonites 4–5 acute; pleonite 5 nearly twice as long as pleonite 4. *Pleotelson* about 25%

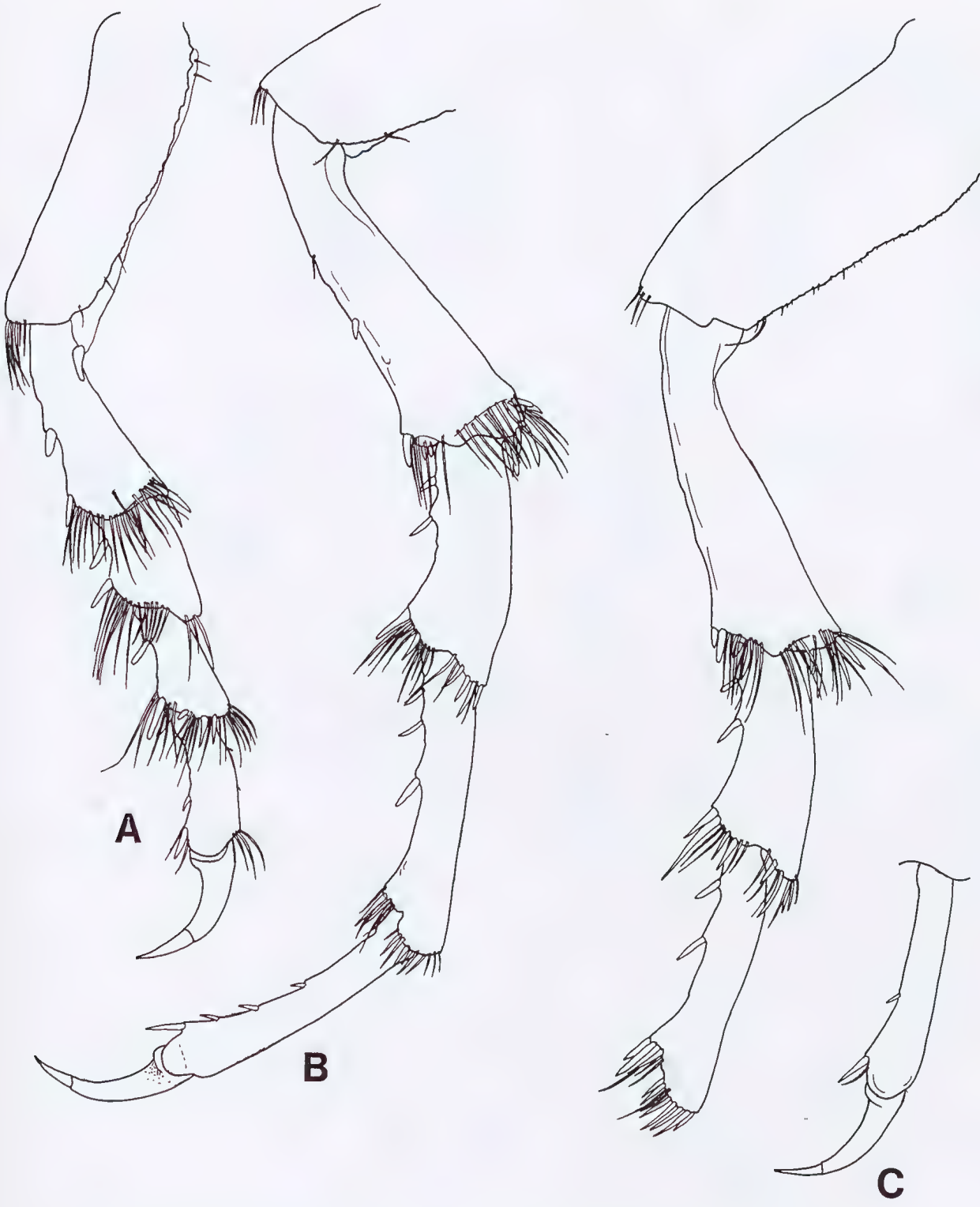

Fig. 3. *Syscenus springthorpei* n.sp., holotype. A, pereopod 4; B, pereopod 6; C, pereopod 7.

BL, 1.2 times as long as greatest width; lateral margins converging smoothly to an acute apex, forming a distinct sub-acute caudomedial point; margins with PMS running from about position of uropod peduncle to apex.

Antennule peduncular article 1 slightly wider (1.2×) than long, with scattered small setae on distal and posterior submarginal surface; article 2 as wide as long, slightly longer than article 1 (1.1×), posterodistal angle with 3 palmate setae; article 3 slightly longer than article 2, 1.6 times as long as wide; flagellum 0.8 times as long as peduncle, extending to posterior of cephalon, with 7 articles, article 1 of which is longest, about 2.2 times longer than article 2. *Antenna* peduncle articles 1–2

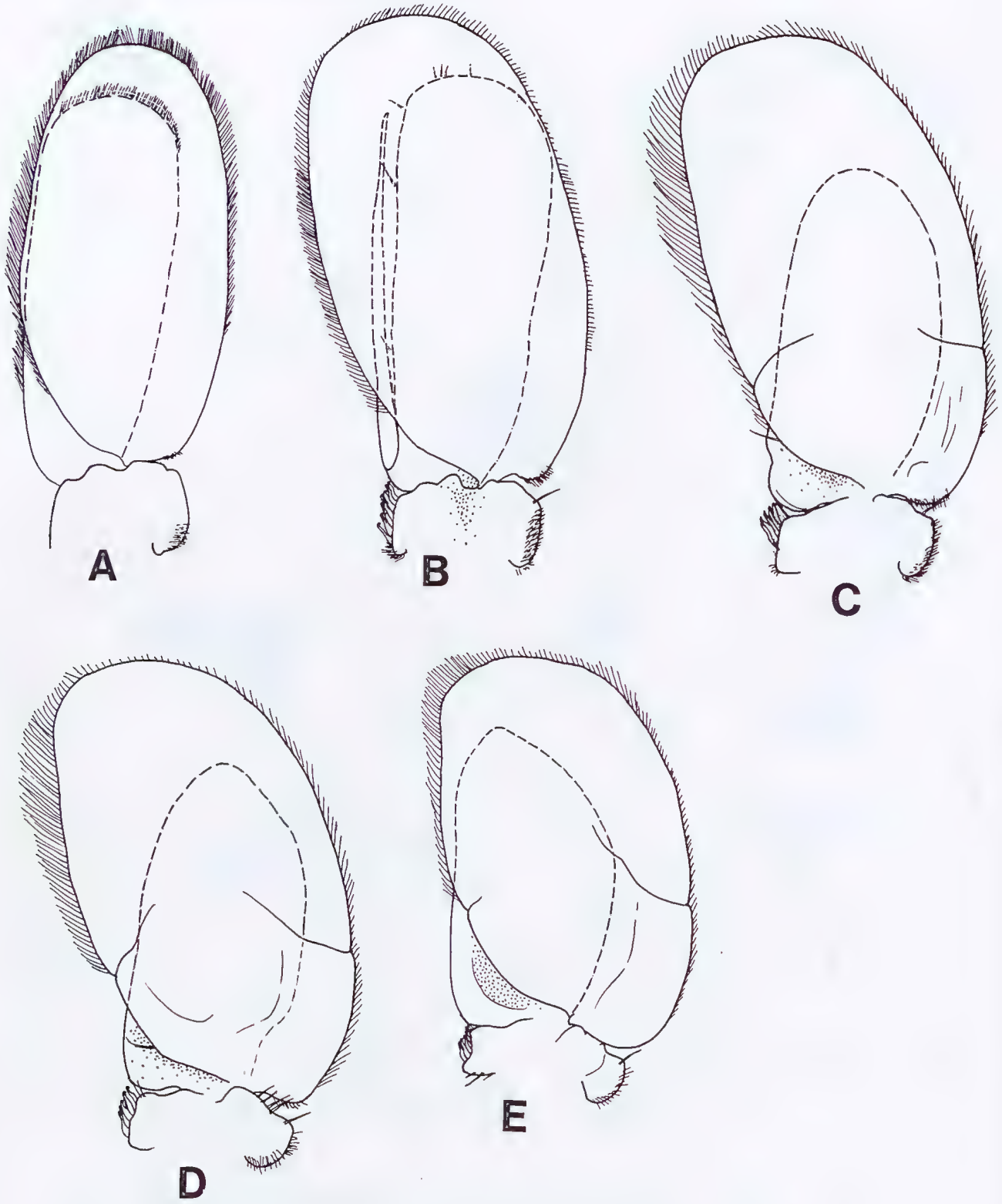

Fig. 4. *Syscenus springthorpei* n.sp., holotype. A–E, pleopods 1–5 respectively.

short, subequal in length; article 3, 2.5 times as long as article 1, 1.25 times as long as wide; article 4, 1.4 times as long as article 3, 1.8 times as long as wide, posterior margin with 13 long PS; article 5 longest, 1.3 times as long as article 4, about 2.7 times as long as wide, posterior margin with 10 long PS; flagellum 1.6 times as long as peduncle, composed of about 20 articles, extending to posterior of pereonite 3; posterior margins of articles 1–11 with long PS.

Frontal lamina anteriorly acute, lateral margins converging posteriorly, not making contact with clypeus.

Mandible incisor falcate; molar process weak; palp article 1 longest, 1.4 times as long as article 2, 1.8 times as long as article 3; article 2 with about 12 long stiff setae at distolateral margin and 3 shorter submarginal setae; article 3 with 9 stout marginal setae, terminal 4 setae being longest. *Maxillule* without small medial lobe, distally with 2 minute simple setae; lateral lobe with 3 terminal and 2 subterminal falcate spines on distal margin. *Maxilla* lateral lobe without spines, medial lobe with 2 weakly hooked spines. *Maxilliped* palp article 1 with distinct distomedial blunt spine, article 2 with 3 spines at distomedial end; article 3 minute, with 2 recurved spines and 2 small simple setae.

Pereopods 1–3 moderately robust, 5–7 moderately elongate; pereopod 4 intermediate between both sets. *Pereopod 1* basis 2.3 times as wide as long, posterodistal angle with dense cluster of simple setae; ischium 0.4 times as long as basis, anterodistal angle with cluster of long simple setae, posterodistal margin with few simple setae; merus short, half as long as ischium, posterodistal angle with 1 large bluntly rounded spine, anterodistal angle with abundant long simple setae; carpus subequal in length to merus, short, 0.38 times as long as propodus, posterior margin with simple setae and 1 large bluntly rounded spine; propodus robust, 1.6 times as long as wide, palm with 1 large bluntly rounded spine opposing dactylus, anterodistal angle with cluster of long simple setae; dactylus long and robust, strongly recurved, 1.3 times as long as propodus. *Pereopods 2* and *3* similar to pereopod 1 but slightly less robust. *Pereopod 4* basis 2.6 times as long as wide, posterodistal angle with dense cluster of long simple setae, posterolateral margin irregularly serrate; ischium 0.7 times as long as basis, 2.3 times as long as wide, posterior margin with 1 large blunt spine medially and 1 at posterodistal angle, distal margin with abundant long simple setae; merus 0.6 times as long as ischium, about 1.3 times as long as wide, posterior margin with large narrowly rounded spine medially and 1 at posterodistal angle, distal margin with long simple setae; carpus subequal in length to ischium, about 2 times as long as distal width, posterior margin with 1 spine, distal margin with 2 spines anteriorly and 3 posteriorly; propodus 1.1 times as long as carpus, about twice as long as wide, posterior margin with 1 short acute spine, posterodistal angle with 1 acute spine, anterodistal angle with 3 simple setae; dactylus subequal in length to propodus, gently curved. *Pereopod 6* basis posterodistal angle with 3 short setae, posterolateral margin irregularly serrate; ischium 3.2 times as long as wide, posterior margin with 1 spine, distal margin with 6 spines anteriorly and 4 posteriorly, with abundant long simple setae; merus 0.6 times as long as ischium, about twice (2.1×) as long as wide, posterior margin with 2 spines, distal margin with 4 spines anteriorly and 3 posteriorly, with long simple setae; carpus 1.4 times as long as ischium, 4.2 times as long as wide, posterior margin with 3 spines, distal margin with 8 spines anteriorly and 5 spines posteriorly; propodus 0.9 times as long as ischium, about 4.7 times as long as wide, posterior margin with 3 acute spines, posterodistal angle with 1 spine; dactylus 0.5 times as long as propodus, slender. *Pereopod 7* similar to 6, but slightly more robust and less spinose; basis 2.4 times as long as wide, posterodistal angle with 3 short setae, posterolateral margin finely serrate, with short simple seta in each indentation; ischium 0.8 times as long as basis, 3.0 times as long as wide, distal margin with 4 stout spines posteriorly, 4 spines anteriorly, with abundant long simple setae; merus 0.6 times as long as ischium, 1.7 times as long as wide, posterior margin with 2 spines, distal margin with 6 spines anteriorly and 4 posteriorly, with few simple setae; carpus 1.3 times as long as ischium, about 2.7 times as long as wide, posterior margin with 2 spines, distal margin with nearly continuous spines, 8 anteriorly and 4 posteriorly; propodus 0.9 times as long as ischium, about 3.7 times as long as wide, posterior margin with 1 spine, posterodistal angle with 2 spines and 1 simple seta; dactylus about 0.6 times as long as propodus, slender.

Penial processes absent, the vasa deferentia opening as slightly raised papillae on surface of sternite 7.

Pleopod 1 exopod 2 times as long as wide, slightly longer (1.1×) than endopod, both rami distally rounded, with continuous PMS (as illustrated); endopod 2.5 times as long as wide; peduncle 1.5 times as wide as long, medial margin with 9 coupling hooks, lateral margin without distinct lobe. *Pleopod 2* 1.1 times as long as pleopod 1, exopod 1.9 times as long as wide, endopod 0.8 times as long as exopod, 2.7 times as long as wide, both rami with PMS (as illustrated); appendix masculina basally inserted, apex not extending beyond ramus, straight, 0.9 times as long as endopod, distally slender; peduncle medial margin with 8 coupling hooks and distally with c. 5 PS, lateral margin with distinct lobe, without PS. *Pleopods 3–5* endopods distinctly smaller than exopods, 0.7, 0.7, and 0.8 times as long as respective exopods, pleopod 3 with PS at distomedial margin, pleopods 4 and 5 without PMS; peduncular medial margins with 9, 7 and 6 coupling hooks respectively, lateral margins distinctly lobate, submarginal row of PS on pereopod 5 only; exopods with continuous PS on 80–90% of margin, rami distally rounded, each with prominent but incomplete transverse suture. *Uropod* rami subequal in length, not extending beyond posterior margin of pleotelson, continuous short PS on lateral and medial margins.

Remarks. *Syscenus springthorpei* can be distinguished from the six other species of the genus by a combination of three characters: the uropods not extending beyond the posterior margin of the pleotelson, the sub-acute caudomedial point of the pleotelson and the antennal flagellum not extending beyond the posterior of pereonite 3. *Syscenus pacificus* and *Syscenus latus* both have a mediodorsal point on one or more of the pleonites. *Syscenus intermedius* is similar, but has a far longer

antennal flagellum and a broadly rounded pleotelson. In general appearance *Syscenus infelix* is most similar, but the pleotelson is distally far more acute with the posterior half of the lateral margins concave and the uropods extend well beyond the pleotelson posterior margin.

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Affinities, Generic Classification and Biogeography of the Australian and New Zealand Mudfishes (Salmoniformes: Galaxiidae)

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ABSTRACT. The Australian mudfish, *Galaxias cleaveri*, resembles the three New Zealand mudfishes (*Neochanna* spp.) in general external morphology. It is the least specialised of a transformation series that includes all four mudfishes, in which the body is elongated, eyes are small, anterior nostrils long, tubular and forward directed, dorsal and anal fins low and long, flanges on the caudal peduncle well developed, pectoral fins small, paddle-shaped, and high on sides behind head, and pelvic fins reduced or lost. Unique specialisations in the vomerine-ethmoid region of the cranium and in the form of the pectoral girdle support the view that these four species are a monophyletic group. The Australian species is therefore included in *Neochanna*. The presence of a marine larval and juvenile life stage in the Australian species (diadromy) probably explains the distribution of the genus, with New Zealand species together derived from the Australian one or their common ancestor by dispersal across the Tasman Sea in prevailing ocean currents. The biogeography of the Australian and New Zealand species is consistent with post-Oligocene geology, and in particular with events during and since the Pleistocene.

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The genus *Neochanna* was established by Günther (1867) to contain a small, cigar-shaped fish found when drains were being dug in swamplands on the West Coast of the South Island of New Zealand; it was described as *N. apoda* (Fig. 1D). While apparently a galaxiid (Galaxiidae) from its posterior dorsal fin and lack of scales, it was distinguished from *Galaxias* species by lacking pelvic fins, having flattened incisor-like jaw teeth, no endopterygoid teeth, long-based and low dorsal and anal fins that are nearly confluent with a distinctly rounded caudal fin, elongated, tubular anterior nostrils that point forwards, and small eyes (McDowall, 1970). Known commonly as "brown mudfish", it became well-known as a fish often found, semi-torpid and aestivating, in damp locations from which water had dried up—beneath logs and stumps, down old root holes around the bases of forest trees, and in similar, damp places where water is ephemeral

(Fitzgerald, 1873; Reid, 1886; Eldon, 1968; McDowall, 1990). Stokell (1949) described a second species of *Neochanna* from the northern North Island of New Zealand—the "black mudfish", *N. diversus* (Fig. 1C)—which shares most of the distinctive features of *N. apoda*, except that its jaw teeth are the typical, recurved somewhat fang-like teeth of other galaxiids, and it occasionally has endopterygoid teeth-though when present they are few and small. It, too, has often been reported as aestivating in locations similar to those reported for *N. apoda* (McDowall, 1990). A third New Zealand species, the "Canterbury mudfish", was described as *Galaxias burrowsius* (Fig. 1B) by Phillipps (1926), and it closely resembles the other mudfishes in many characters. It was excluded from *Neochanna* by both Phillipps (1926) and Stokell (1949) because it possesses pelvic fins, though these are much smaller than in other New Zealand *Galaxias* (and have only 4–5 rays, compared with 7 in most species) and it also has a few, if very small, endopterygoid teeth. Like *N. diversus* it has conical, fang-like jaw teeth. McDowall (1970) included the Canterbury mudfish in *Neochanna* because of the several distinctive similarities between the three species. He considered that they formed a radiation within the New Zealand Galaxiidae, and preferred to group these species on the basis of relationship indicated by shared derived characters, even though doing so meant that absence of pelvic fins was no longer an explicit diagnostic character of the genus. All three species show a trend towards anguilliform characteristics, being least specialised in the Canterbury mudfish and most specialised in the brown mudfish.

Australia also has a species commonly known as "Tasmanian mudfish", originally described as several species from Tasmania (*G. cleaveri* Scott, 1934, *Saxilaga anguilliformis* Scott, 1936, and *G. upcheri* Scott, 1942), but these were treated as a single species, *G. cleaveri*, by McDowall & Frankenberg (1981) (Fig. 1A). This species has since been found also on Flinders Island, in Bass Strait (Green, 1984), and in southern, coastal Victoria (Jackson & Davies, 1982; Koehn & O'Connor, 1990; Koehn & Raadik, 1991); the Victorian populations are separated from Tasmanian populations by Bass Strait (see Fig. 10).

McDowall (1969, 1970, 1990) drew attention to obvious external similarities between the Australian *G. cleaveri* and New Zealand *Neochanna* species, and discussed the prospect that they are phylogenetically more closely related to each other than any of them is to other galaxiids. McDowall & Frankenberg (1981) commented only that *G. cleaveri* resembles New Zealand *Neochanna* and did not further discuss or investigate their relationships.

This paper explicitly addresses that question and presents a cladogram that expresses an hypothesis of these relationships on the basis of common, distinctive, derived characters. It examines the biogeography of the mudfishes, in the context of the proposed phylogeny.

Methods and material examined

Study is based on unregistered material in the NIWA fish archive of galaxiid fishes, including both whole preserved specimens and cleared and alizarin-stained osteological specimens, listed in Appendix 1. The cladogram derived from the study, presented in Fig. 9, was produced using HENNIG86 (Farris, 1988) and CLADOS (Nixon, 1991). Alternative character states used in analysis are listed in Table 1 and a coding matrix for these is in Table 2.

Results

1. Identification of outgroup for determination of phylogenetic relationships: Fruitful examination of relationships depends in part on the appropriate choice of outgroups for determining the distinctiveness and polarity of morphological characters. The closest relatives of the mudfishes within the Galaxiidae are not obvious. The four species form a transformation series from least to more specialised (Fig. 1A-D) with the Australian species the least specialised and most *Galaxias*-like. They possess no identified characters that point to a relationship with any of the other, usually more specialised and distinctive, galaxiid genera such as *Brachygalaxias, Galaxiella* and *Nesogalaxias*. Amongst the distinctive features of the Australian mudfish is the presence of a diadromous (amphidromous) life cycle (McDowall, 1988, 1993) involving spawning in fresh water, a larval migration to sea, life there for several months, followed by a return migration of small juveniles to fresh water (Fulton, 1986). This is considered to be a primitive feature in the Galaxiidae (McDowall, 1993), and hence a common ancestry of the mudfishes and other amphidromous species seems likely within the family Galaxiidae; derivation from some non-diadromous species is less likely since a return to a diadromous life history is then required. Five other known diadromous *Galaxias*, viz. *G. truttaceus* Valenciennes (Australia), *G. brevipinnis* Günther (Australia, New Zealand), *G. fasciatus* Gray, *G. argenteus* (Gmelin) and *G. postvectis* Clarke (all New Zealand) share numerous apparently primitive characters in the genus. From amongst these, the Australian *G. truttaceus* was used for cladistic analysis as an outgroup for determining character polarities within the mudfishes. However, use of any of the above species, or all five of them together, would have produced an identical result.

2. External morphology: The three New Zealand and one Australian mudfishes resemble each other and differ from most other galaxiids in the following combination of external, macroscopic characters (Fig. 1A-D):

- elongate, cigar-shaped form with dorsal and ventral body profiles near parallel from head to tail (other than sometimes a deepening of the belly in mature to ripe fish prior to spawning);

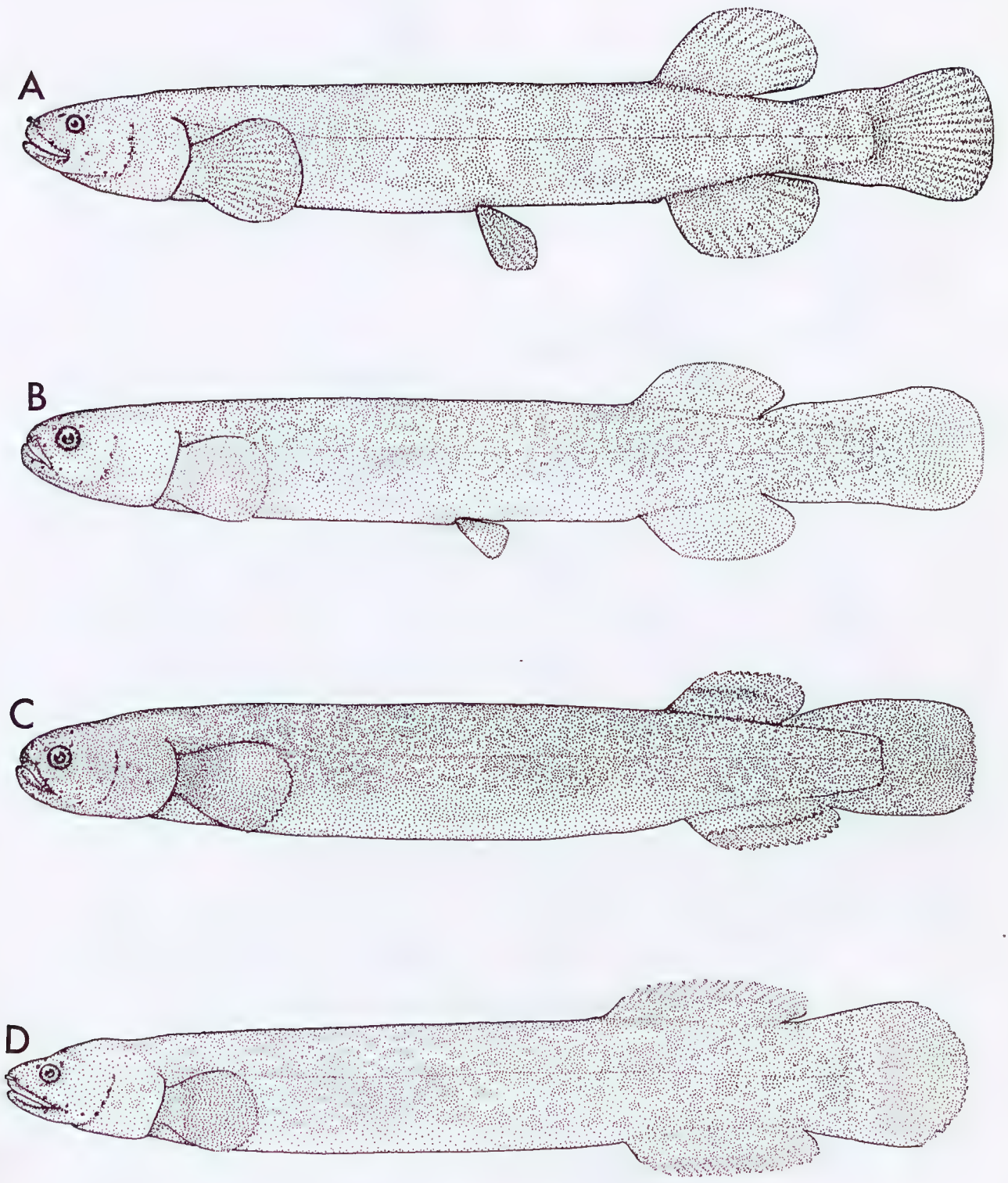

Fig. 1. The four galaxiid mudfishes: **A**, Australian mudfish—*Neochanna cleaveri*, Pieman River, Tasmania, 79 mm T.L.; **B**, Canterbury mudfish—*N. burrowsius*, Gawler Downs, Hinds River, N.Z., 108 mm T.L.; **C**, Black mudfish—*N. diversus*, swamp at Waiharara, 112 mm T.L.; **D**, Brown mudfish—*N. apoda*, tributary of Mangatarere Stream, Ruamahanga River, 110 mm T.L.

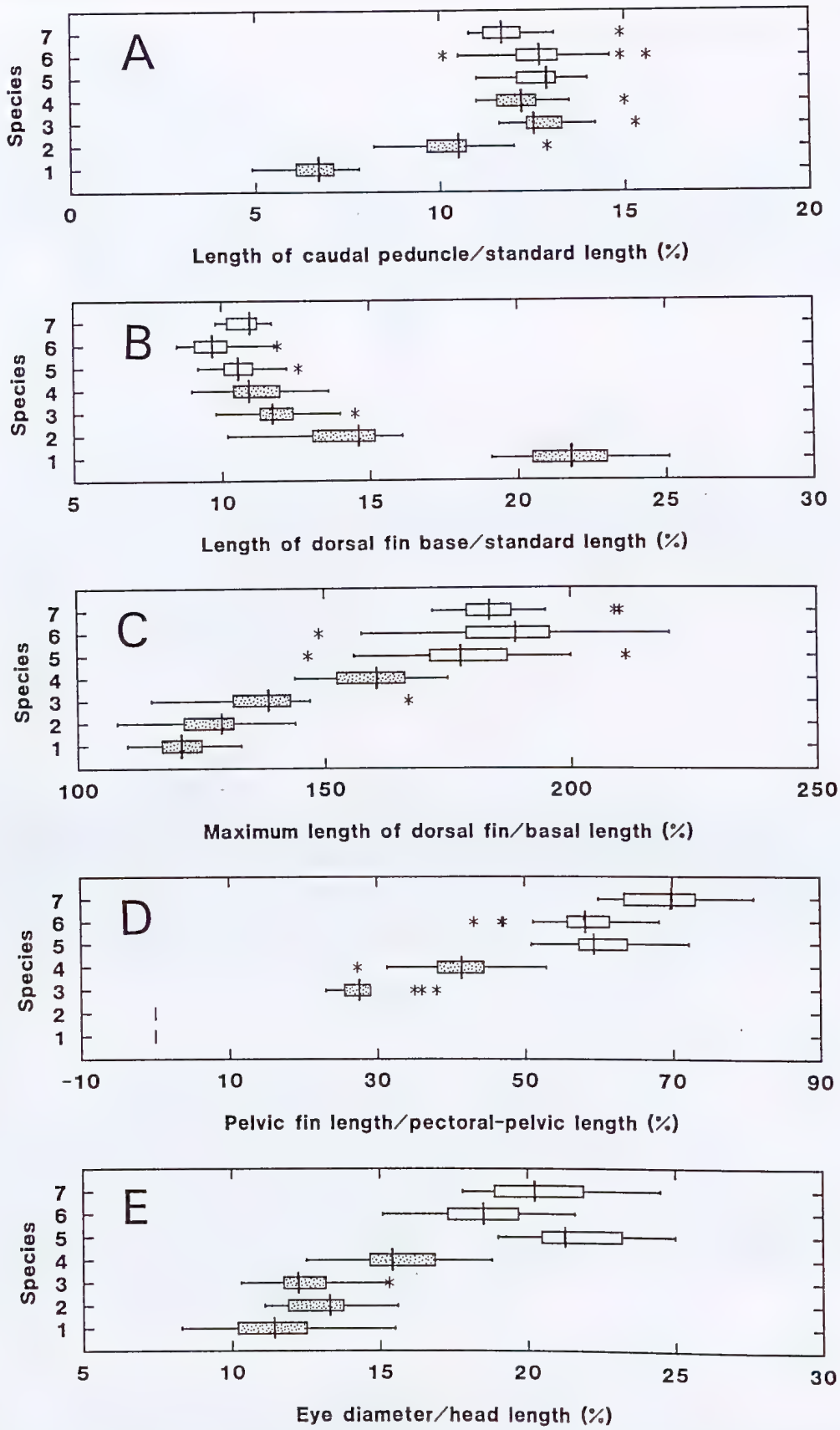

Fig. 2. Morphometric ratios in *Neochanna* species (stippled) and selected *Galaxias* species: **A**, length of caudal peduncle/S.L. (%); **B**, length of dorsal fin base/S.L. (%); **C**, maximum length of dorsal fin/basal length of fin (%); **D**, pelvic fin length/pectoral-pelvic length (%); **E**, eye diameter/head length (%): 1 *Neochanna apoda*, 2 *N. diversus*, 3 *N. burrowsius*, 4 *N. cleaveri*, 5 *Galaxias truttaceus*, 6 *G. brevipinnis*, 7 *G. fasciatus*—data from McDowall (1970) and McDowall & Frankenberg (1981). Plots use the box-plot facility in SYSTAT (Wilkinson, 1990) and show median, interquartile range (box), and 1.5 times interquartile range; asterisks are outside values.

- small eyes (Fig. 2E) set well below the dorsal head profile;
- elongate, tubular, anterior nostrils that project forward over the upper lip;
- pectoral fins small and rounded, distinctly lateral in position and behind the opercular openings, fin base broad, upper edge of fin towards lateral line and the first ray forming the upper edge of the fin (in most *Galaxias* these fins are low on the sides, almost below the rear of the opercular openings, and they face downwards in almost shark-like fashion (Fig. 3); the first pectoral ray, which articulates with the scapula, rotates forward to form the leading edge of the fin);
- caudal fin rounded.

There is also a series of distinctive character trends among the four species:

- strongly developed flanges may occur along the dorsal and ventral edges of the caudal peduncle, as a result of which the dorsal, caudal and anal fins tend to be confluent, or nearly so; this character is least developed in the Australian mudfish, but is increasingly evident in Canterbury, black and brown mudfishes (Fig. 1A-D);
- dorsal and anal fins are rather long (Fig. 2B) and low with the same trend of increasing development of this character in the four species; the distal fin margins are distinctly rounded and middle rays the longest (and thus most *Galaxias*-like) in the Australian species, but fins are progressively longer, lower, and flatter, with the distal edge tending to be parallel with body profile and all fin rays of similar length in the Canterbury, black and brown mudfishes (Figs 1A-D, 2C);
- pelvic fins are reduced in size in the Australian species, sometimes have 6, but usually have 7 rays as in most *Galaxias*; the Canterbury mudfish has even more reduced pelvic fins that have 4 or more usually 5 rays; brown and black mudfishes have no pelvic fins or girdle at all (Fig. 2D);
- endopterygoid teeth are reduced but present in the Tasmanian species, and similarly in the Canterbury mudfish, usually absent in the black mudfish and few and small when present, but always absent in the brown mudfish.
- the brown mudfish differs from all others in having flattened, incisor-like jaw teeth, and also large specimens tend to have a strongly-developed, eel-like, muscular dome behind the occiput.

All these species thus have "anguilliform-like" characteristics, that could be interpreted as providing adaptation for life in a "crevice" habitat filled with aquatic vegetation and debris. Small eye size is reflected in a high ratio of forebrain/optic lobes in the brain of the three New Zealand species compared with most other New Zealand Galaxiidae (Cadwallader, 1975; Fig. 4). Comparable data have not been published for the Australian species.

There is thus a suite of characters affecting several independent morphological systems in which there are

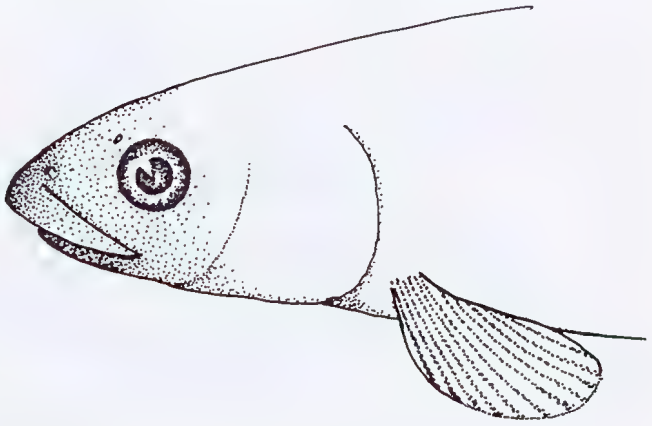

Fig. 3. Rotated and down-turned pectoral fin, as in *Galaxias postvectis* (compare with Fig. 1).

clear similarities between the four species. The issue for resolving the species' relationships and generic taxonomy is to determine the extent to which these various characters indicate homologies based on phylogenetic relationship in two or more species and/or are convergent similarities that are due only to the adoption of a similar life style.

Not all of these distinctive characters are uniquely present in these species in the Galaxiidae. The Tasmanian *G. parvus* Frankenberg, for instance, has long tubular nostrils, pelvic fins of reduced size with fewer than seven pelvic rays, and a somewhat rounded caudal fin (McDowall & Frankenberg, 1981); it is commonly called "swamp galaxias" (Fulton, 1990). *Galaxias rekohua* Mitchell, newly described from the Chatham Islands of New Zealand (Mitchell, 1995), has strongly developed flanges on the caudal peduncle with dorsal, caudal and anal fins nearly confluent. Several species of *Galaxias* have elongate, tubular, cigar-shaped body form though, more often than not, these are species adapted for swifter-flowing streams and life within a boulder/cobble substrate (e.g., *G. brevipinnis*, *G. paucispondylus* Stokell in New

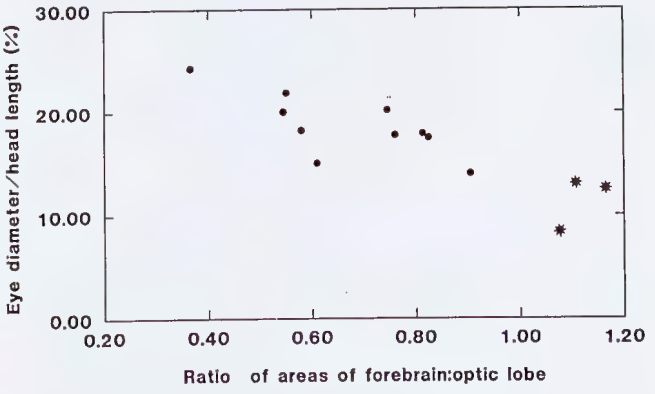

Fig. 4. Relationship between eye size and relative sizes of forebrain and optic lobe in New Zealand *Galaxias* (•) and *Neochanna* (*) (data from Cadwallader, 1975).

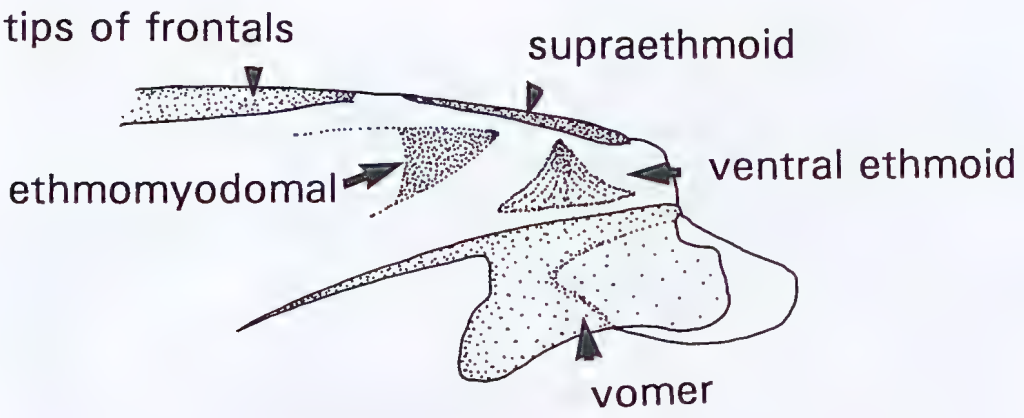

Fig. 5. Lateral view of ethmoid region in *Galaxias fasciatus* (note ventral position of vomer).

Zealand—McDowall, 1970). *Galaxias prognathus* Stokell and *G. paucispondylus* have small eyes, also, though not as small as in the mudfishes (McDowall, 1970). However, the mudfishes have both a higher level of modification in each these various characters, and have all of them together, and thus a unique combination of derived characters.

3. Osteology: Examination of the osteology of galaxiids reveals distinctive, independent specialisations in at least two character complexes in the four mudfishes.

Vomerine-ethmoid region of cranium: McDowall (1969) drew attention to a suite of particularly distinctive osteological characters in the ethmoid region of the three New Zealand species of *Neochanna*.

In most *Galaxias*, the frontals extend forwards over the orbits, but become well separated anteriorly, as they diverge over the ethmoid region. The ethmoid region (Fig. 5, 6A) consists of a block of cartilage that is a central brace for the anterior cranium and upper jaw. On top of the ethmoid cartilage is a perichondral supraethmoid which lies anterior to the tips of the frontals and behind the tip of the cranium; below the ethmoid cartilage is an endoskeletal ventral ethmoid. There is sometimes a small ethmomyodomal. The vomer is a flattish bone, almost butterfly-shaped, which sits directly below the ventral ethmoid, and has a posterior shaft that extends back to join the parasphenoid. The ethmoid cartilage has two blunt cartilaginous spurs on each side. One of these, the "maxillary spur" is low on the ethmoid cartilage which projects anterolaterally just above the wings of the vomer to form a brace for the head of the maxilla; this, in turn, rests inside the ascending process of premaxilla. Thus, this spur supports the medial upper jaw. The spurs are also well separated in *Galaxias* (Fig. 6B). In all four mudfishes the ascending process of the premaxilla fits between the forward projecting arms of the Y-shaped anterior ethmoid cartilage and vomer. The ascending process of the premaxilla projects back and up towards but not over the anterior ethmoid region. The other, "palatine spur," originates higher on the ethmoid cartilage, and projects antero-lateroventrally to meet a cup-shaped anteromedially, inward and upward pointing tip of the palatine.

The four mudfishes though somewhat variable, nevertheless show a consistent series of differences (Fig. 6B, C). There are no endoskeletal median ethmoid ossifications (supraethmoid, ventral ethmoid, ethmomyodomal). In the Australian, brown and black mudfishes, the frontals meet anteromedially and project forwards across the ethmoid cartilage to its front. The vomer is large and somewhat Y-shaped from above (conforming to the anterior ethmoid cartilage which is also Y-shaped), and it folds upwards around the anterior of the ethmoid cartilage to almost meet the tips of the frontals. The maxillary spur, that is cartilaginous in *Galaxias* and the Australian mudfish, becomes ossified in these three New Zealand mudfishes, providing an increasingly robust support for the upper jaw.

The ethmoid cartilage and vomer have the same shape and ossification in the Canterbury mudfish, but the frontals do not project forwards, to cover the ethmoid cartilage and almost meet the vomer anterodorsally, as they do in the other three species.

The anterior tip of the palatine retains its association with the lateral spur of the ethmoid cartilage in Tasmanian, brown and Canterbury mudfishes. However, in the black mudfish additional ossification of the ethmoid cartilage has extended to include the "palatine spur" and the anteromedial surface of the palatine has established a firm association with the side of the vomer/ethmoid ossification, further strengthening the anterior of the cranium (Fig. 6C).

Thus, though varying somewhat in details, there is in all four mudfishes a unique and consistent turning

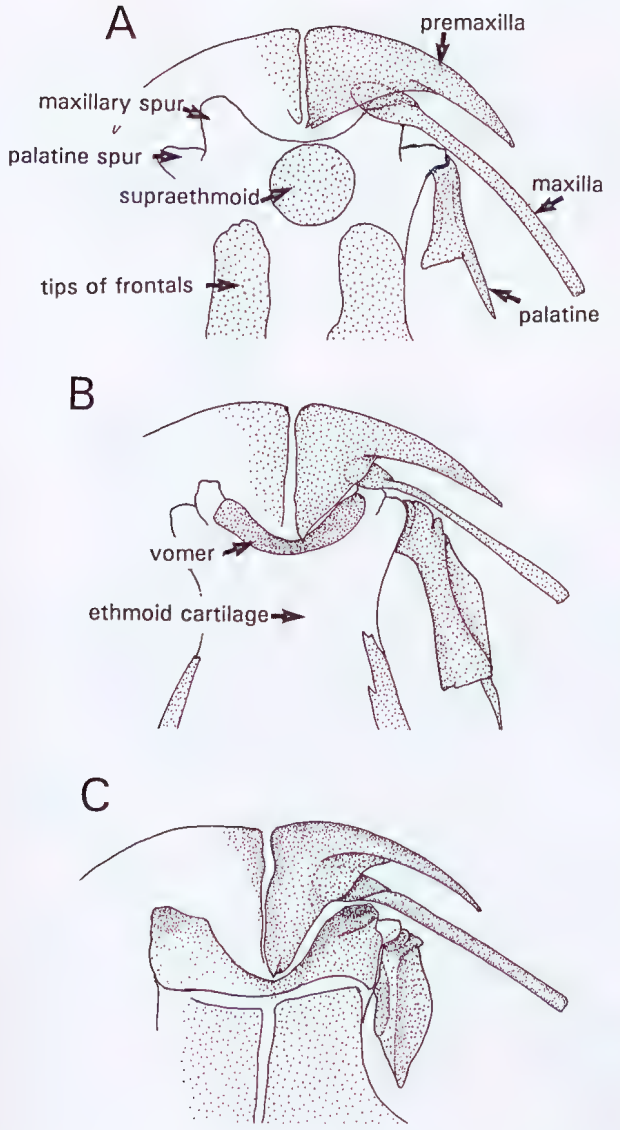

Fig. 6. Osteology of the ethmoid region in: **A**, *Galaxias fasciatus*; **B**, *Neochanna burrowsius*; **C**, *N. diversus*.

upwards of a Y-shaped vomer to enfold the anterior of the cranium, and increased ossification of the junction between, and a closer association between the upper jaw, palatine, and ethmoid/vomerine region of the cranium.

Ecologically these structural features make sense in a fish that lives in intimate relationship with the substrate and/or in debris-strewn waterways, as is true of all four species. The structure appears to be designed to strengthen and consolidate the upper jaw/ethmoid region of the cranium by increasing ossification and providing closer proximity of bones.

Pectoral girdle: In most *Galaxias*, the pectoral girdle consists primarily of the perimeter of a broad semicircle (Fig. 7A). The post-temporal connects dorsally with the supraoccipital, and in a series the post-temporal, supracleithrum, and cleithrum curve outwards and backwards, downwards, and then forwards and inwards following the body wall immediately behind the opercular opening, running nearly parallel to the opercular membrane. There is a weak pectoral symphysis in the mid-ventral isthmus, where the pointed tips of the two cleithra meet (Fig. 8A). The coracoid is a substantial L-shaped bone that lies largely medial to the cleithrum, and has a long horizontal ramus that extends forwards to meet inside the tips of the cleithrum at about the pectoral symphysis. Thus the two cleithra and two coracoids (left and right) all meet at or near, and form, the mid-ventral pectoral symphysis. The shorter, vertical ramus of the coracoid projects upwards inside, and meets the cleithrum and a small scapula which sits above the four pectoral radials; the scapula and radials support the bases of the pectoral fin rays, the first ray on the scapula and the others on the radials.

In all four mudfishes, the form of the coracoid and the relationships of the coracoid and cleithrum are distinctly different. The post-temporal, supra-cleithrum and cleithrum (Fig. 7B), form an arc about parallel to the opercular membrane, similar to that of other galaxiids. But the coracoid is a much smaller bone, that is essentially triangular in shape, having lost the vertical ramus. The horizontal ramus is short and meets the cleithrum about half its length back from the pectoral symphysis, and so reaches nowhere near the tips of the cleithra and is quite separate from the pectoral symphysis. Ossification in the coracoid does not meet that of the scapula, but the coracoid and scapula form ossifications in a cartilaginous plate that supports the radials and thence the fin rays. In only *N. diversus*, at the junction between the anterior tip of the coracoid and the cleithrum, there is a distinct, small knob that forms the articulation with the coracoid (Fig. 8B).

Study of other *Galaxias* suggests that the form and articulations of the coracoid are specialisations uniquely derived in the four mudfishes. There are other *Galaxias* with distinctly lateral pectoral fins, such as *G. parvus* (Tasmania) and *G. maculatus* (Australia, New Zealand and South America). These are mid-water swimming species. They retain the L-shaped coracoid, which joins the cleithrum at the pectoral symphysis, as in *G. truttaceus, G. brevipinnis* and *G. fasciatus*. Thus there has not been modification of the pectoral skeleton in response to the more lateral placement of the pectoral fins. All four mudfishes thus appear to have a uniquely modified pectoral girdle in the shape of the coracoid and its articulation with the cleithrum.

Discussion

While it might be argued that all of the "systems" indicating similarity between the four mudfishes, and their differences from *Galaxias*, are associated with a changed mode of life, the distinctive features of the mudfishes involve several organ systems and include diverse aspects of general morphology (body form, tail and fin shapes, nostrils, eye size), upper jaw/vomerine/ethmoid osteology, and pectoral girdle. In particular, the osteological details associated with at least two organ

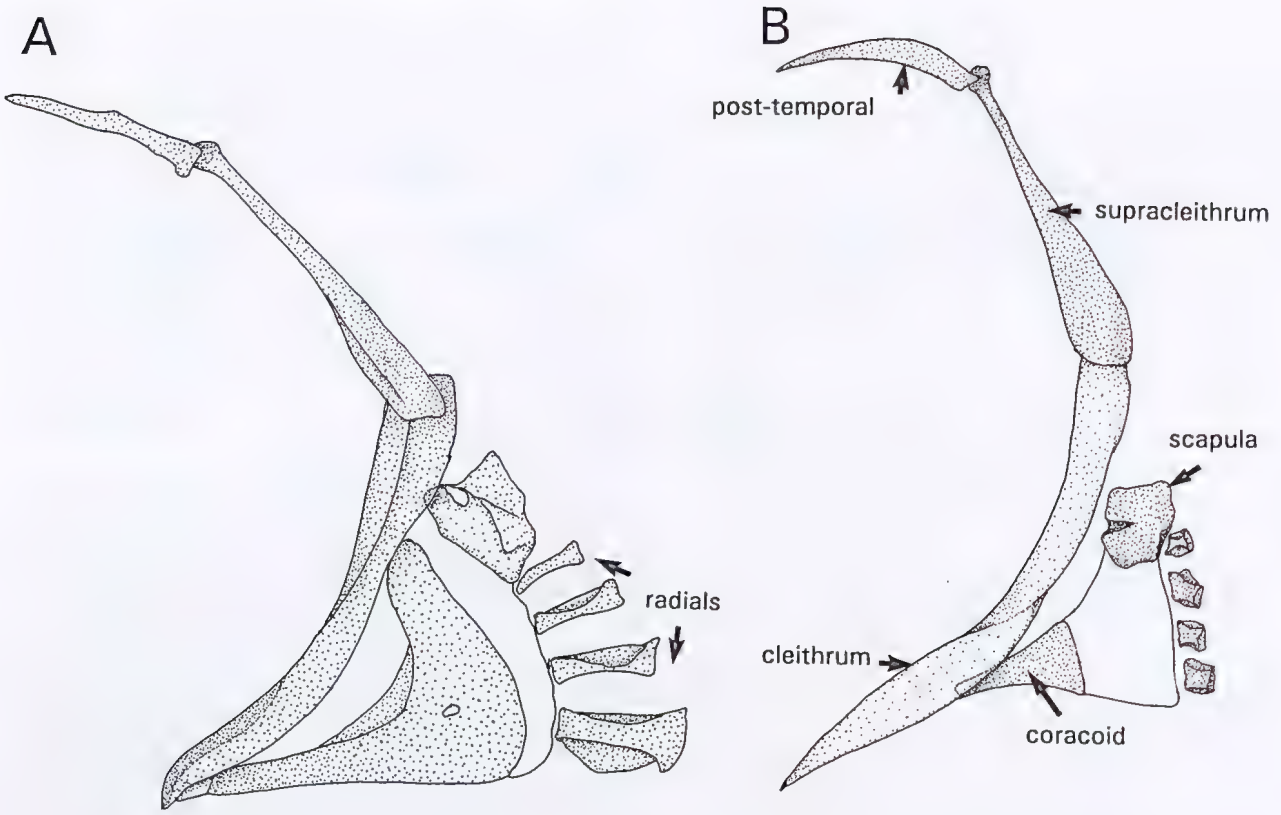

Fig. 7. Lateral view of osteology of pectoral girdle in: **A**, *Galaxias fasciatus*; **B**, *Neochanna diversus*.

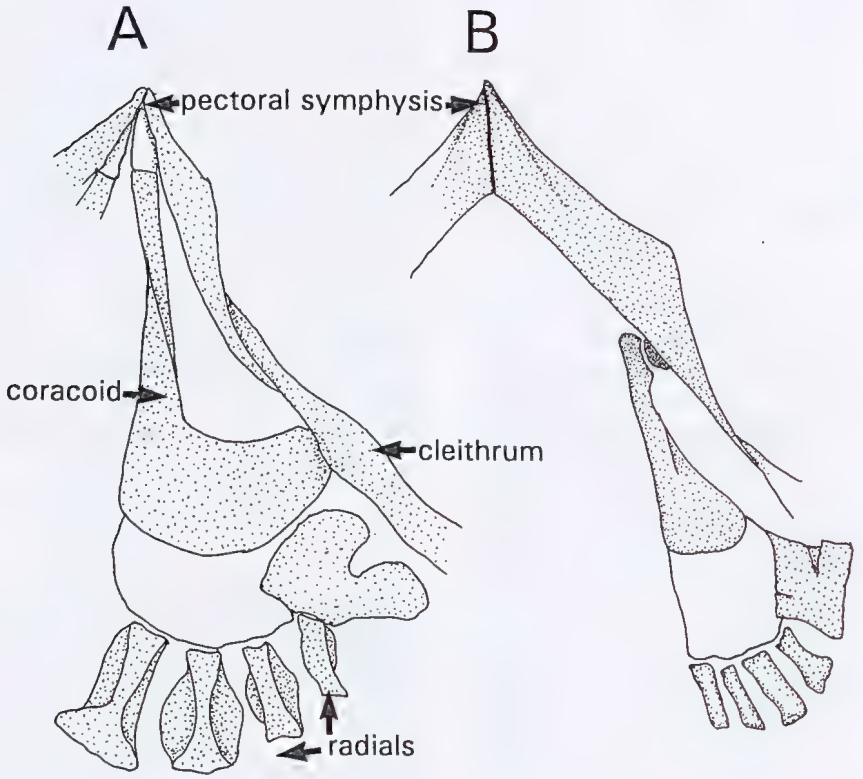

Fig. 8. Ventral view of osteology of pectoral girdle in: **A**, *Galaxias fasciatus*; **B**, *Neochanna diversus*.

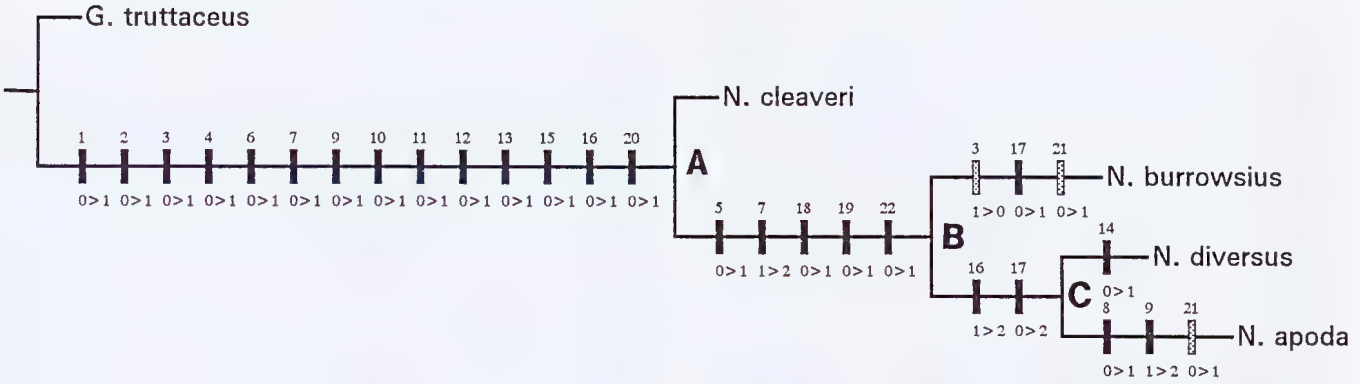

Fig. 9. Cladogram showing hypothesised relationships of *Neochanna* species (length 28, consistency index 0.92, retention index 0.75). A black box indicates an apomorphic character; a shaded box indicates a homoplastic character. Superscripts refer to characters and subscripts indicate direction.

systems are distinctive and very similar in all four species. This suggests that the four mudfishes have a common derivation, and that they are more closely related to each other than any one or more of them is related to other Galaxiidae. They are thus considered to form a monophyletic group. It is appropriate that the Tasmanian mudfish be transferred from *Galaxias* to *Neochanna* to reflect this relationship.

Where in the Galaxiidae these four mudfishes have their closest relationships is at present uncertain. The Tasmanian mudfish is clearly the least specialised of the four species, and one of its probably primitive characteristics is its retention of a diadromous life cycle (Fulton, 1986; McDowall, 1988). If diadromy is a primitive feature of the family that reflects its ancient salmoniform relationships (McDowall, 1993), then it is also likely that the closest relatives of the mudfishes are other diadromous *Galaxias*. The Tasmanian mudfish is much the least specialised of the mudfishes.

The data generated two nominally equally valid cladograms, only one of which is shown in Fig. 9. In the alternative the positions of *N. burrowsius* (Phillipps, 1926) and *N. diversus* were switched (*N. burrowsius* and *N. apoda* together shared a common ancestor with *N. diversus*). The characters that supported these alternative arrangements were:

- presence (*N. burrowsius*) or absence (*N. diversus* and *N. apoda*) of pelvic girdles and fins, and
- whether there are 16 principal caudal fin rays as in most species of *Galaxias*, or less than 16 rays.

Characters that support the cladogram are discussed below, including reasons why the phylogenetic evidence based on pelvic girdle and fins is preferred to that from caudal fin ray counts (see "NODE C"), below. Nodes mentioned are inserted in Fig. 9 as capital letters.

NODE A: Taking the diadromous species of *Galaxias* discussed above as an outgroup, *Neochanna* (now including *N. cleaveri*, as well as *N. burrowsius, N. diversus* and *N. apoda*) stands as a monophyletic group (Fig. 9) defined by the following characters:

a. vomer folds up the anterior wall of the ethmoid cartilage (Fig. 6B) (Character State CS.1 in Table 1);
b. loss of endoskeletal ethmoid ossifications (CS.2 in Table 1);
c. frontals advance across the ethmoid cartilage to the anterior of the cranium (in all but *N. burrowsius*) (Fig. 6B) (CS.3);
d. anterior tubular nostrils elongated, anteriorly directed (Fig. 1A-D) (CS.6);
e. eyes small (Figs 1A-D, 2E) (CS.7);
f. endopterygoid teeth reduced (though this is a poor indicator of relationships as it is variable within at least *N. diversus*, in which teeth are sometimes absent, but if present are few and small) (CS. 9)
g. pectoral fins small, laterally positioned (Fig. 1A-D) (CS. 10,11);
h. coracoid articulates with cleithrum well back from the pectoral symphysis (Fig. 7B, 8B) (CS. 12);
i. pelvic fins reduced (Figs 1A-D, 2D) (CS. 16).

NODE B: Synapomorphies that define a subgroup comprising the three New Zealand mudfishes—*N. burrowsius, N. diversus* and *N. apoda*—include:

j. maxillary spurs in ethmoid cartilage ossified (Fig. 6B) (CS. 5);
k. pelvic fin rays reduced from 7 to 5 or fewer (*N. burrowsius*), or fins and girdles lost (*N. apoda* and *N. diversus*) (CS.17);
l. dorsal and anal fins long and low, with fin rays subequal in length along fin (alternate character is fins high and rounded with central rays longest, as in the Australian mudfish) (Fig. 1A-D) (CS. 18);
m. flanges on upper and lower margins of caudal peduncle extend forwards from caudal fin to reach bases of dorsal and anal fins, the three fins becoming more or less confluent (Fig. 1A-D) (CS. 19);
n. loss of diadromous life history with no marine life stage (CS. 22).

These characters establish the three New Zealand species as a monophyletic group and therefore suggest a single derivation from an ancestry common with that of the Australian *N. cleaveri*.

An alternative hypothesis could be that the advance of the frontals (CS. 3) is a synapomorphy common to *N. cleaveri, N. apoda* and *N. diversus*, with the condition in *N. burrowsius* plesiomorphic. This would require that the putative synapomorphies, listed above as uniting the three New Zealand species (CS. 5, 17, 18, 19, 22), each evolved twice, and this is rejected as being far less parsimonious. The condition of the frontals in *N. burrowsius* is therefore seen as secondary and its similarity to *Galaxias* a homoplasy.

NODE C: If a group comprising the three New Zealand mudfishes is accepted as monophyletic, then their interrelationships are interpreted as *N. apoda* and *N. diversus* together being a sister group of *N. burrowsius*, on the basis of the following characters:

o. eye size further reduced (Fig. 2E) (CS. 2);
p. pelvic fins and girdle completely lost (present though reduced in *N. burrowsius*) (Fig. 1B-D) (CS. 16)
q. caudal peduncle is also reduced in length (Fig. 1B-D), but was not included in the cladistic analysis because of broad overlap.

This hypothesis requires reduction of the number of principal caudal rays from the standard 16 in most galaxiids independently in both *N. apoda* (13–16 rays) and *N. burrowsius* (11–14 rays) (it remains at 16 in *N. diversus*). The alternative is that reduction in caudal fin rays is a synapomorphy in these two species, but this requires independent total loss of the pelvic fins and girdle in *N. apoda* and *N. diversus*, and still requires independent retreat of the frontals from above the ethmoid cartilage in *N. burrowsius*. Since caudal fin ray number in *N. apoda* is sometimes the standard 16 and sometimes less, the process of loss can be seen occurring in that species and independent reduction in both *N. apoda* and *N. burrowsius* is therefore likely.

I have not found unique independently derived specialisations in the Australian *N. cleaveri*, by comparison either with other *Neochanna* or with *Galaxias*. This is not true of the New Zealand species, in which the following autapomorphies are evident:

Autapomorphies in *N. apoda* include:

- flattened, incisor-like teeth in jaws (CS. 8);
- total loss of endopterygoid teeth (CS. 9);
- also, dorsal and anal fin bases are much elongated and increased ray counts (Fig. 1D, 2B & C); and
- caudal peduncle is very short (Fig. 1D, 2A)

Autapomorphies in *N. diversus* include:

- closer association between palatine and side of ethmoid cartilage (Fig. 6B) (CS. 4);
- presence of knob on cleithrum for articulation of coracoid (Fig. 8B) (CS. 14);
- broad pectoral symphysis (Fig. 8B) (CS. 15).

Autapomorphies in *N. burrowsius* include:

- retreat of frontals from above ethmoid cartilage (CS. 3);
- reduction in caudal fin ray count to only 13–14 (CS. 21).

Biogeography of the genus *Neochanna*

Trans-Tasman range of *Neochanna*: The close phylogenetic relationships between the Australian and New Zealand mudfishes, hypothesised above, raises biogeographical implications only hinted at in previous studies (McDowall, 1970; McDowall & Frankenberg, 1981). Any hypothesis employing land-based mechanisms of vicariance/dispersal for *Neochanna* implies an ancient, probably late Mesozoic/early Tertiary, land connection between Australia and New Zealand involving the former existence of Gondwana and its subsequent fragmentation and dispersal around the southern hemisphere. A scenario involving the occurrence of the common ancestors of the Australian and New Zealand mudfishes on Gondwana, and their separation by a vicariance event occurring perhaps as long as 85 million years ago (Cooper, 1989), is conceivable, and perhaps consistent with scenarios presented for the biogeography of other taxa common to Australia and New Zealand.

However, given the fact that the Australian mudfish is diadromous and thus has a marine juvenile life-stage probably lasting several months, and given the fact that ocean currents sweep across the Tasman Sea from Australia to New Zealand, an origin of the mudfishes in Australia, with dispersal to New Zealand in these ocean currents is an equally likely scenario. This is consistent with the hypothesised phylogeny of the genus, in which the Australian species is the most primitive and the sister group of the three more derived New Zealand species.

Choosing between these scenarios is not simple. Some would argue that congruence of distribution patterns between disparate and unrelated taxonomic groups points

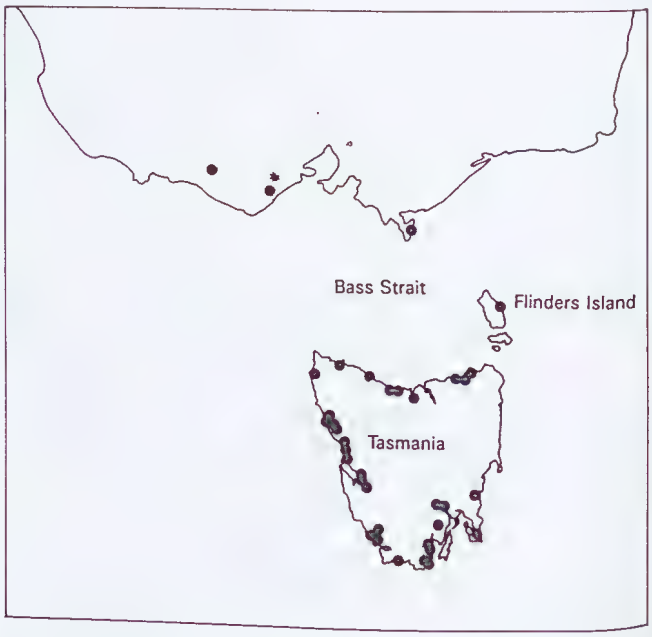

Fig. 10. Distribution of Australian mudfish, *Neochanna cleaveri* (* Wye River).

conclusively to a common vicariance-related, explanation for the distributions (Croizat *et al.*, 1974; Rosen, 1974; Craw, 1989). I am not, however, of the view that such common patterns necessarily have the same explanations or that dispersal explanations should be invoked only when phylogenies are inconsistent with possible patterns of vicariance suggested by other taxa (Croizat *et al.*, 1974; Rosen, 1974; see McDowall, 1978; Andersson, 1996). Berra *et al.* (1996) have recently reported on results of electrophoretic comparisons of populations of *G. maculatus* from Australia, New Zealand and South America, and they concluded that in this diadromous species differences between populations over its vast range are so slight as to suggest recent, and even continuing, gene flow—though this is not a new idea (McDowall & Whitaker, 1975; McDowall, 1978). The only way this is possible is by transoceanic dispersal in the southern ocean. If this is possible for *G. maculatus* between Australia/New Zealand and South America, dispersal of the diadromous Australian mudfish from eastern Australia to New Zealand is also highly conceivable.

Distribution of the Australian species: The Australian mudfish occurs primarily in Tasmania, though there are records from Flinders Island (Bass Strait—Green, 1984), and in coastal, southern Victoria (Jackson & Davies, 1982; Koehn & O'Connor, 1990; Koehn & Raadik, 1991—Fig. 10). Freshwater fish distributions that span Bass Strait occur also in other Australian species. Some are diadromous, like *G. maculatus, G. brevipinnis* and *G. truttaceus* (Galaxiidae—McDowall & Frankenberg, 1981), *Prototroctes maraena* Günther (Prototroctidae—McDowall, 1996a), *Anguilla australis* Richardson and *A. reinhardtii* Richardson (Anguillidae—Beumer, 1996), and *Pseudaphritis urvillii* Cuvier and Valenciennes (Bovichtidae—Andrews, 1996). Others, however are not diadromous, such as *Galaxiella pusilla* (Mack) (Galaxiidae—McDowall & Frankenberg, 1981) and *Nannoperca australis* Günther (Nannopercidae—Kuiter *et al.*, 1996). The distributions of the diadromous species may be explained by either dispersal of marine life stages through the sea across Bass Strait, between the Australian mainland and Tasmania, or by the known presence of a land connection across the strait as recently as the Pleistocene (<14,000 years before present—Davies, 1974). The same alternative dispersal explanations are unlikely to apply to the non-diadromous species and the land bridge scenario is a much more likely explanation for these.

Choosing between these scenarios to explain the distribution of the Australian mudfish (which is diadromous—Fulton, 1986) is, again, not simple; either mechanism seems equally plausible. Koehn & Raadik (1991) suggested that the known distribution of the Australian mudfish in Victoria "closely conforms to the region formerly encompassed by a land bridge" across Bass Strait, and from that I infer that they favoured a causal relationship. They thought that if the occurrence of the fish in Victoria was due to marine dispersal, "the species would be expected to be more widely distributed", thus tending to discount the role of diadromy in the species' presence in Victoria. On the other hand, they stated that "geomorphological conditions that existed during and after the last glaciation... restricted non-diadromous freshwater species" as a result of which "only diadromous species inhabit the short coastal streams. The diadromous life cycle of *G. cleaveri* accounts for its distribution in the Wye River" (Fig. 10*). They thereby apparently attribute the range of the species in Victoria to diadromy. Moreover, they were also equivocal about the nature of its diadromy, suggesting that the "more restricted distribution of *Galaxias cleaveri* [compared with other diadromous *Galaxias* species] suggests that the larvae may be confined to estuaries". Thus they appear to attribute the presence of the Australian mudfish in Victoria to the presence of a land connection, but its distribution in Victoria perhaps to a diadromous life cycle and therefore perhaps dispersal through the sea. Dispersal across Bass Strait by a marine stage of the Australian species seems, to me, a viable option.

Distribution and biogeography of the New Zealand species: Any interpretation of New Zealand historical biogeography must be structured around the fact that its land mass has had a "rough tectonic history" (Gibbs, 1989). In particular, there was very little emergent land during the Oligocene, about 30 million years ago, perhaps so little that virtually the entire biota dates from post-Oligocene dispersal to New Zealand, if Pole (1994) is correct. Thus, all terrestrial and freshwater taxa must, at least, have passed through a very severe evolutionary bottleneck, with intensive and extensive taxonomic "winnowing" and extinction at that time (Cooper, 1989; Cooper & Cooper, 1995). What we observe, today, results from speciation and dispersal of the survivors of that event/period, as well as the addition of taxa that have dispersed to the New Zealand region since then and have speciated as the land area increased again. The effects of any more ancient events, and in particular the supposed influences of "terranes" of allochthonous origins on the distributions of biotic elements (Gibbs, 1989) are bound to have been profoundly altered by the reduced land area of the Oligocene, as well as later marine transgression, mountain building, land connections and volcanism, to the extent that today's taxa and their distributions are unlikely still to reflect their origins in such terranes (Cooper, 1989; Cooper & Cooper, 1995).

If we assume a single ancestry/common derivation of the New Zealand species as shown in the cladogram in Fig. 9, then the biogeography of the genus *Neochanna* in New Zealand is structured around the speciation and divergence of that single ancestral stock. Distributions of the three New Zealand mudfishes are entirely allopatric, with:

- *Neochanna diversus* present in the north of the North Island;
- *N. apoda* in the western and southern North Island and West Coast of the South Island, and
- *N. burrowsius* in the eastern South Island (Fig. 11).

None of the three species is diadromous (though their common ancestor may have been), so that their present distributions will probably not have been affected by

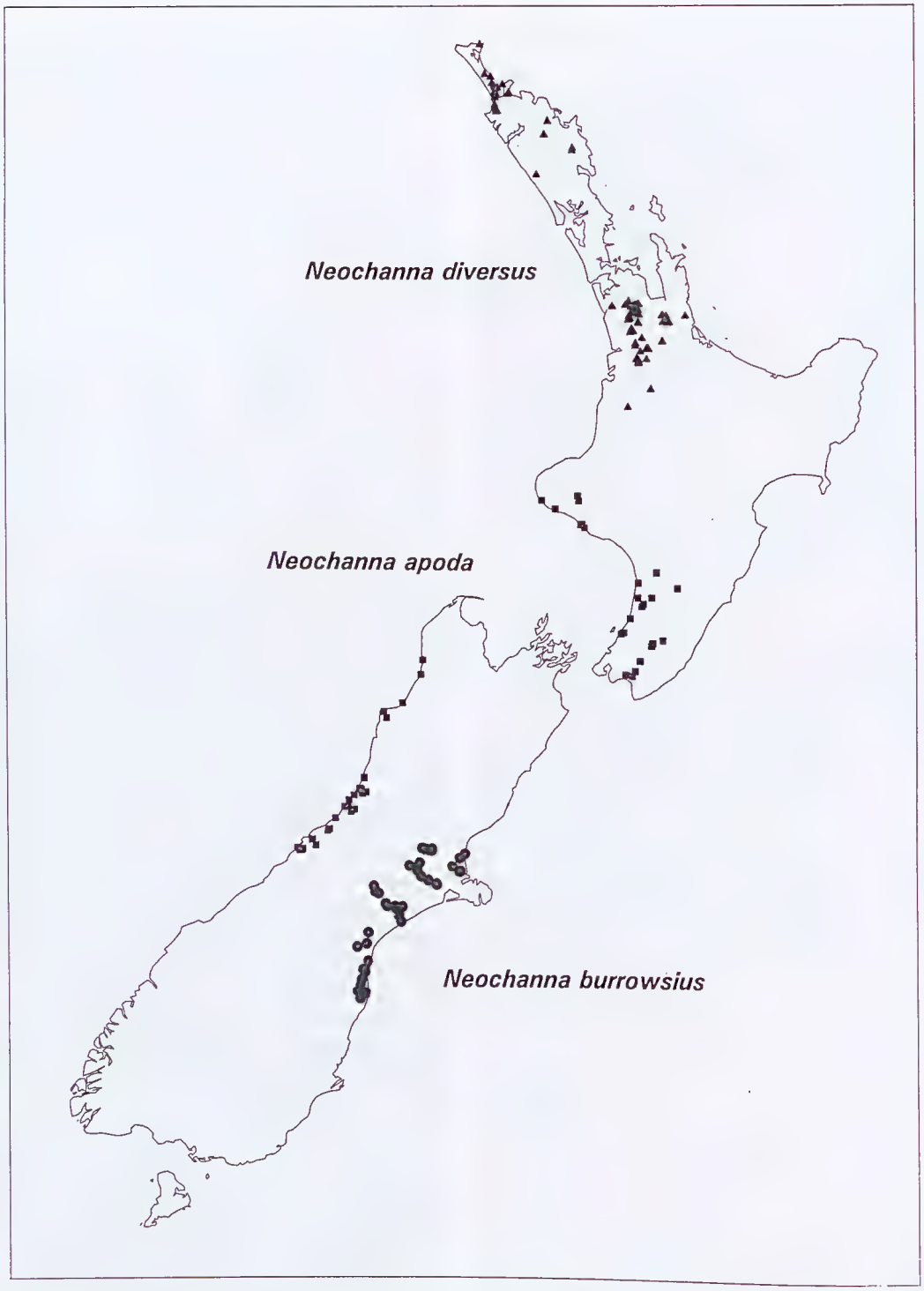

Fig. 11. Distribution of the three New Zealand mudfishes, *Neochanna apoda, N. burrowsius*, and *N. diversus* (data from NIWA New Zealand Freshwater Fish Database).

recent or continuing dispersal of marine life stages through the sea. They are likely therefore to reflect, at least in part, the geological history of the landscape—probably over late Tertiary to Recent times. Likely influential events in this geological history include the following:

- the fact, noted above, that most of the New Zealand region was submerged beneath ocean during Oligocene times, about 30 million years ago with emergent land of minimal size, (Cooper, 1989, and Cooper & Cooper, 1995 show only several relatively small emergent islands—Fig. 12);
- the Kaikoura orogeny during the Pliocene and early Pleistocene, that resulted in the uplifting of the present mountain ranges of New Zealand, particularly of the Southern Alps (which bisect the South Island distributions of *N. apoda* to the

north-west of the Alps and *N. burrowsius* to the south-east) (Fig. 11);

- formation of the Canterbury Plains during the late Pliocene and Pleistocene, as the product of extensive erosion and outwash from the rising Southern Alps;
- extensive marine transgression across the now southern half of the North Island during the Pliocene and early Pleistocene, when there was sea across the present North Island almost as far north as Lake Taupo; however, parts of the south-western present North Island are thought to have been connected to the northern tip of the South Island at that time, but separated by sea from the rest of the North Island (Fig. 13);
- re-emergence from the sea of the above area, and the closure of all sea connections across central New Zealand during the Pleistocene, at a time of lowered sea levels (Fig. 14);
- later reopening of the sea connection across central New Zealand at what is now known as Cook Strait;
- extensive Pleistocene to Recent glaciation, with permanent snow and ice to low levels, especially along the West Coast of the South Island;

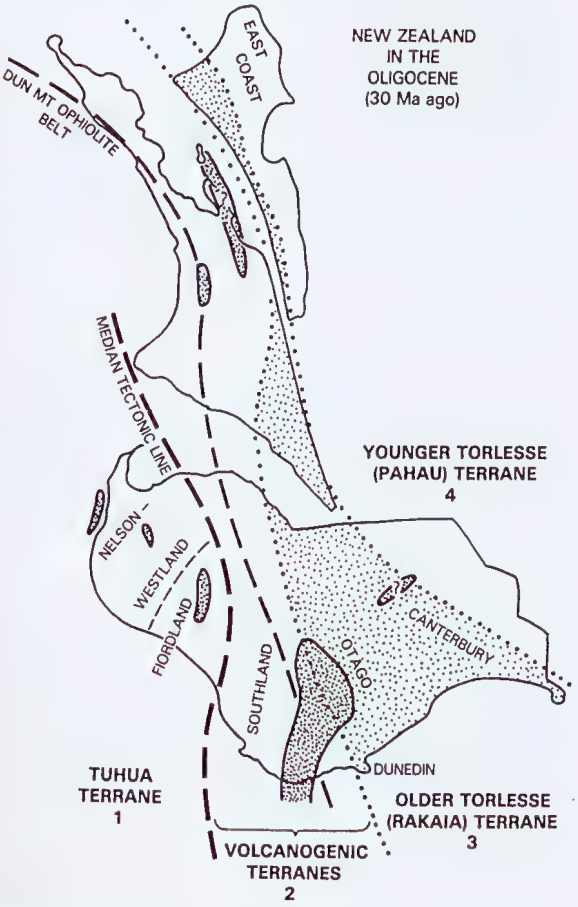

Fig. 12. The New Zealand area during the Oligocene (c. 30 million years ago): dark stippling indicates areas considered to have been above sea level (from Cooper, 1989).

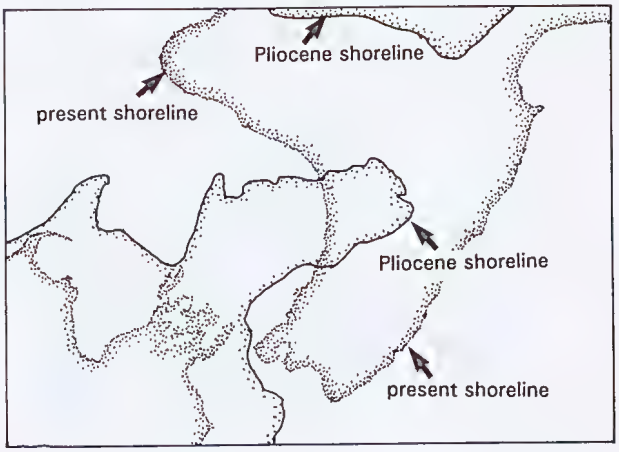

Fig. 13. New Zealand during the Pliocene, showing extensive marine transgression across the southern North Island (redrawn from Lewis & Carter, 1994).

- intensive Pleistocene to recent volcanism in the central/northeastern North Island (from about 25,000 years ago).

(These events are described variously by Suggate *et al.*, 1978; Fleming, 1979; Gage, 1980; Stevens, 1980; Wilson & Walker, 1985; Cooper, 1989; Wilson & Houghton, 1993; Lewis & Carter, 1994; Cooper & Cooper, 1995.)

In examining the biogeography of the mudfishes in New Zealand, it is important to know the extent to which present distributions are a product of these various known geo-historical events that affected the landscape and its biota, as opposed to the influences of any more ancient processes.

The three species of *Neochanna* could have been isolated on the various Oligocene islands (Fig. 12), and have spread from these centres as the New Zealand land mass emerged from the sea during the mid-Tertiary. Such a scenario would probably have required a distinct "Canterbury" island (Cooper, 1989, shows a possible such land area—Fig. 12), particularly if the phylogeny of New Zealand mudfishes, with the Canterbury mudfish a sister group of the two others, as presented in Fig. 9, is accepted.

Alternatively, however, the total allopatry of the three species is consistent with the hypothesis that their distributions reflect relatively recent (late Tertiary and since) geological history. Where distributions seem consistent with such more recent events, it is probably appropriate in the first instance to assume that there are causal relationships. The scenario developed here is offered on that basis, and again under the assumption that the phylogenetic relationships of the three species to the Australian species, and to each other, are as proposed above (Fig. 9), i.e. that *N. apoda* and *N. diversus* are sister species, and together form a sister group of *N. burrowsius*.

How far spread *Neochanna* was in New Zealand prior to the uplift of the Southern Alps is, of course, unknown.

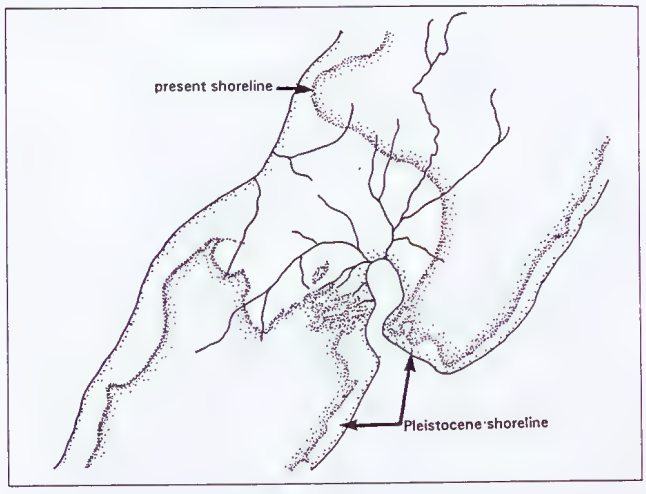

Fig. 14. Central New Zealand during the Pleistocene, indicating likely confluences of river systems between North and South Islands as a result of lowered sea levels (redrawn from Fleming, 1979).

One possibility is that the common ancestor of *N. apoda* and *N. diversus*, and perhaps the common ancestor of all three species, was widespread, perhaps as far north as the Waikato and even Northland prior to the Pliocene marine transgression across the southern North Island (Fig. 13). *Neochanna burrowsius* is now separated from *N. apoda* in the South Island by the Southern Alps, the uplift of which can be interpreted as a major vicariant event (Fig. 11).

The present distribution of *N. diversus* (Northland, south through the Hauraki Plains, and Waikato as far as the Mokau River) equates closely with the proto-North Island of Pliocene times of extensive marine transgression (Fig. 13: Fleming, 1979; Lewis & Carter, 1994), which may suggest that the fish was already in that area before the marine transgression developed. *Neochanna diversus* does not occur in the eastern North Island (Bay of Plenty), and this is consistent with the east coast of the North Island having not adopted its present connections to the remainder of the North Island until less than 10 million years ago (Cooper, 1989). Mudfish may never have reached the region. Alternatively, if there were any populations of mudfish there, they may have been extirpated by events relating to volcanism known to have occurred in the central/eastern North Island over the past 25,000 years (Wilson & Houghton, 1993; Wilson & Walker, 1985; McDowall, 1996b). Other non-diadromous North Island freshwater fishes that might have been expected in the north-east (Bay of Plenty/East Cape) are notably sporadic in distribution east of about the longitude of Coromandel (McDowall, 1990, 1996b), and so absence of mudfish is not inconsistent with this.

The Pliocene marine transgression of the southern North Island would have excluded all freshwater fishes (and all other terrestrial and freshwater biota) from that area, but *N. apoda* may have occupied the continuous land from the Wellington peninsula southwards through the northern West Coast of the South Island (Fig. 13), to the northwest of the Southern Alps. Following retreat of the seas, re-emergence of the southern North Island, and perhaps also with bridging of Cook Strait as recently as 10,000–20,000 years ago (Lewis & Carter, 1994), there was ample opportunity for *N. apoda* to disperse north into the southern and western North Island, undoubtedly assisted by confluence of river systems that drained the south-western North Island and northern South Island (Fig. 14). As a result, *N. apoda* now occurs along the west coast of the North Island almost as far north as Cape Egmont (or did until locally extirpated by human impacts), in the Wairarapa in and south of the Manawatu River system, as well as widely in the West Coast of the South Island (Fig. 11). The northern part of this distribution equates closely with river systems that are believed formerly to have drained the emergent land before Cook Strait took its present conformation in quite recent times (Fig. 14). Distribution of *N. apoda* extends well south along the West Coast of the South Island. There seem to be no existing habitat-suitability reasons why the fish should not occur further south. However, as Main (1989) has shown, extensive Pleistocene glaciation probably extirpated all terrestrial and freshwater life in the southern West Coast, including any populations of *N. apoda*. This mudfish occurs there only north of about the estimated limits of low elevation glaciation.

Neochanna burrowsius occurs only as far south as the Waitaki River, and is thus confined largely to the Canterbury Plains. Dispersion of *N. burrowsius* southwards, as the plains were formed by erosion and outwash of gravels from the uplifting Southern Alps to the west during the late Pliocene, Pleistocene to Present, seems a likely scenario. Its absence south of the Waitaki, i.e. in the ancient, long emergent, Otago peneplain to the south, suggests that it was never present there. Nor does it occur in Central Otago or the Southland Plains, where there are plenty of apparently suitable habitats. The absence of any mudfish from southern New Zealand is consistent with a more northern origin of *N. burrowsius* with dispersion south as far as the Waitaki, as the Canterbury Plains were formed during late Pliocene to recent times.

Overall, the patterns of distribution and speciation of the three New Zealand mudfishes conform easily to a scenario established around the late Tertiary and subsequent geological history of New Zealand. In the absence of evidence to the contrary, the small radiation of these species appears to be of about that age; there is nothing presently known that suggests a much more ancient, Gondwana, origin. The prospect that the common ancestor of all four mudfishes in Australia and New Zealand was a Gondwana form, which survived the Oligocene bottleneck in New Zealand (Cooper & Cooper, 1995), and which dispersed and speciated in New Zealand in response to these same late Tertiary and subsequent geo-historical events, discussed above, cannot

be excluded. Dating of speciation events, particularly the separation of the Australian and New Zealand lineages, using DNA sequencing technology may provide an estimate of the time of divergence of the New Zealand species from *N. cleaveri* in Australia, and thereby throw light on this question, and allow a more rigorous choice of historical scenarios for the origins, distribution and speciation of the genus *Neochanna*.

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Appendix 1: Material examined includes unregistered material in the fish archive of the National Institute of Water and Atmospheric Research, and material from the collections of the Museum of New Zealand (NMNZ), as follows (* signifies cleared and alizarin-stained osteological preparations, for which fish lengths are given: this material is substantially the same as that used by McDowall, 1969).

Galaxias argenteus: *(1), Lake Brunner, Grey River system, N.Z., no date, 160 mm S.L.; (2), Pita Creek, Manakaiaua River, N.Z., ? January, 1984, 93–94 mm S.L.

Galaxias brevipinnis: *(2), Lake Kiriopukae, Waikaremoana, N.Z., 63–68 mm S.L.; (6), Ohau River, upper Waitaki River system, N.Z., 13 March, 1991, 66–87 mm S.L.; *(1), Kangaroo River, N.S.W., Australia, 8 January, 1976, 75 mm S.L.

Galaxias fasciatus: *(3), locality and date unknown, N.Z., 63–156 mm S.L.; (4), small drain feeding Mahakaiawa Stream, N.Z., 15 April, 1971, 51–114 mm S.L.

Galaxias maculatus: *(1), Waikanae River, N.Z., no date, 64 mm S.L.; (3), Otaki River, N.Z., 16 October, 1964, 65–70 mm S.L.

Galaxias postvectis: (3), Stony Creek, Kaniere River, Hokitika River system, Westland, N.Z., 147–189 mm S.L.

Galaxias truttaceus: (6), Lake Dudley, Tasmania, 25 February, 1978, 69–113 mm S.L.; *(2), locality unknown, Tasmania, no date, 62–79 mm S.L.; *(2), locality unknown, no date, 55–81 mm S.L.

Neochanna apoda: *(5) Kaipaitangata Stream, ? March, 1965, 58–69 mm S.L., spring at Dalefield, 2 July, 1968, 55–81 mm S.L., both locations Ruamahanga River system, N.Z.; (2) Opunake, N.Z., June, 1926, 146–152 mm, NMNZ P1557, (3) Rongotea, N.Z., February 1958, 85–100 mm, NMNZ P2485.

Neochanna burrowsius: *(1) and (16) Buchanan Creek, tributary of Waihao River, South Canterbury, N.Z., 6 July, 1976, 85 mm S.L. and 39–109 mm S.L.; (3) creek at Eiffelton, south of Ashburton, N.Z., no date; NMNZ P4891, 65–125 mm S.L.

Neochanna cleaveri: *(1) Pieman River, Tasmania, Australia, 28 January, 1964, 56.5 mm S.L.; *(2), unknown locality, Tasmania, Australia, no date, 60, 86 mm S.L.; (4), Derwent River, Tasmania, Australia, 20 March, 1987, 43–52 mm S.L.

Neochanna diversus: *(1), swamp, lower Waikato River, New Zealand, no date, 85 mm S.L.; (6), drain at Te Kauwhata, Waikato River, N.Z., 20 July, 1966, 27–45 mm; (22) swamp at Waiharara, Awanui River system, N.Z., 25 March, 1965, 40–134 mm, NMNZ P4898.

Table 1. Definition of primitive and derived character states: assignment of characters as primitive (0) or derived (1 & 2) is based on outgroup comparisons with *Galaxias* species, and is discussed in the text

1. Vomerine/ethmoid region of anterior cranium:
   0 vomer flat and lies largely below ethmoid cartilage;
   1 vomer folds up anterior wall of ethmoid cartilage to meet frontals (Fig. 6B).
2. Ethmoid ossification
   0 endoskeletal ethmoid ossifications present;
   1 no endoskeletal ethmoid ossifications.
3. Frontals:
   0 diverge anteriorly and do not reach forward to meet vomer;
   1 joined anteriorly and extend forward to meet vomer that folds up ethmoid cartilage.
4. Palatine spur on ethmoid cartilage:
   0 spur cartilaginous, no ossification;
   1 spur ossified.
5. Maxillary spur on ethmoid cartilage;
   0 spur cartilaginous, no ossification;
   1 spur ossified.
6. Anterior tubular nostrils:
   0 short and oblique;
   1 long and directed forwards.
7. Eyes:
   0 large;
   1 moderate;
   2 small.
8. Jaw teeth:
   0 sharp, recurved, fang-like;
   1 flattened and incisor-like.
9. Endopterygoidal teeth:
   0 large and numerous;
   1 variable, few and small, or absent;
   2 always absent.
10. Pectoral fin size:
   0 large;
   1 small.
11. Pectoral fin position:
   0 low on sides, facing downwards;
   1 high on sides, facing laterally.
12. Coracoid articulation in pectoral girdle:
   0 coracoids long, articulate with cleithrum at pectoral symphysis;
   1 coracoids shortened, articulate with cleithrum well back from pectoral symphysis.
13. Coracoid shape:
   0 coracoid large and distinctly L-shaped, also articulating with cleithrum near scapula;
   1 coracoid small and triangular; does not articulate with cleithrum near scapula.
14. Cleithrum:
   0 cleithrum has no knob at articulation with anterior ramus of coracoid;
   1 cleithrum has bony knob at articulation with anterior ramus of coracoid.
15. Pectoral symphysis:
   0 narrow and weak;
   1 broad and strong.
16. Pelvic fin size:
   0 large, usually > 50% of pectoral-pelvic interval;
   1 small, usually < 50% of pectoral-pelvic interval;
   2 fins and girdle lacking.
17. Pelvic fin rays:
   0 usually 7 rays;
   1 usually 5 rays;
   2 no rays, fin lacking.
18. Dorsal and anal fin shape;
   0 fins high and rounded, bases short;
   1 fins long and low, distal margin nearly parallel to body profile, bases long.
19. Caudal peduncle flanges:
   0 flanges weak, not reaching rear of dorsal and anal fin bases;
   1 flanges long, confluent, or nearly confluent with dorsal and anal fin bases.
20. Caudal fin shape:
   0 caudal fin emarginate to truncate;
   1 caudal fin distinctly rounded.
21. Caudal fin rays:
   0 nearly always 16 rays; variation slight;
   1 13–16 rays, variable;
   2 11–14 rays, variable.
22. Diadromy:
   0 present;
   1 absent.

Table 2. Matrix of character states in *Galaxias truttaceus* (outgroup) and *Neochanna* species; 0 = ancestral condition, 1 & 2 = derived conditions, characters as numbered in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Galaxias truttaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neochanna cleaveri	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	0	0	1	0	0
Neochanna burrowsius	1	1	0	1	1	1	2	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Neochanna apoda	1	1	1	1	1	1	2	1	2	1	1	1	1	0	1	2	2	1	1	1	1	1
Neochanna diversus	1	1	1	1	1	1	2	0	1	1	1	1	1	1	1	2	2	1	1	1	0	1

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Bones and Muscles of the Suspensorium in the Galaxioids and *Lepidogalaxias salamandroides* (Teleostei: Osmeriformes) and their Phylogenetic Significance

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ABSTRACT. The phylogenetic position of the south-western Australian endemic, *Lepidogalaxias salamandroides*, has been controversial since its description by Mees in 1961. Some workers place this tiny fish with the galaxioids of the southern end of the Southern Hemisphere, one considered it to be an esocoid (a group otherwise restricted to the northern end of the Northern Hemisphere), while another hypothesises that it may be the sister group of the Neoteleostei. My study of the suspensorium and its muscles in associated euteleosts supports the hypothesis that the galaxioids are monophyletic and include *Lepidogalaxias*. Data from the bones and muscles of the suspensorium suggests the following pattern: ([Retropinnidae + Prototroctidae] + [*Lepidogalaxias* + (Galaxiidae + Aplochitonidae)]). *Lepidogalaxias* is the sister group of Galaxiidae + Aplochitonidae based particularly on synapomorphies of the adductor mandibulae. The suspensorium and its muscles in *Lepidogalaxias* and the other galaxioids are described in detail for the first time. I also critically evaluate competing hypotheses of galaxioid relationships and comment on paedomorphosis in the group.

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The salmoniform fishes endemic to the Southern Hemisphere, the galaxioids, include the Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae (all *sensu* McDowall, 1969). Although the familial arrangement may vary, except for Rosen (1974) most recent workers consider the galaxioids to be monophyletic (e.g., McDowall, 1969, 1984; Nelson, 1972; Fink, 1984; Howes & Sanford, 1987; Williams, 1987; Begle, 1991; Nelson, 1994). In contrast, Rosen (1974) linked the Galaxiidae + Aplochitonidae (his Galaxiidae) with the Salmonidae, and the Retropinnidae + Prototroctidae (his Retropinnidae) with the Osmeridae + Plecoglossidae + Salangidae.

Although most agree that the galaxioids are monophyletic, the phylogenetic position of the tiny galaxioid-like south-western Australian endemic, *Lepidogalaxias salamandroides*, is controversial. When Mees (1961) first described this highly unusual fish he

placed it in its own genus within the Galaxiidae, but suggested that it might occupy a separate subfamily. Scott (1966) reviewed the features of *Lepidogalaxias* and compared them to the Galaxiidae. He tentatively left it in the Galaxiidae but suggested that it may belong in a new family. McDowall (1969), in a review of Southern Hemisphere salmoniforms stated that it was not a galaxiid. Frankenberg (1969) described the osteology and some soft anatomy of *Lepidogalaxias*. Although he noted that it shared several morphological similarities with the esocoids of the Northern Hemisphere, he concluded that the overall evidence favoured a galaxiid relationship. He placed it in its own family, Lepidogalaxiidae, and suggested dividing Galaxioidei (of Greenwood *et al.*, 1966) into two superfamilies, one to contain *Lepidogalaxias* (Lepidogalaxioidea), and the other the remaining galaxioids (Galaxioidea). In a study of cephalic sensory canals and pit lines Nelson (1972: 38) concluded that "The relationships of *Lepidogalaxias* remain obscure" but noted that it shared similarities with both the Galaxiidae and Aplochitonidae (*sensu* McDowall, 1969) and the esocoid *Dallia*. Rosen (1973) placed the Lepidogalaxiidae in the suborder Salmonoidei of the order Salmoniformes, but did not discuss its relationship to the other salmonoids (Salmonidae, Galaxiidae, Aplochitonidae, Retropinnidae, Salangidae, Osmeridae, and Plecoglossidae).

In a radical departure, Rosen (1974) presented evidence that *Lepidogalaxias* was an esocoid, and placed it in the Esocoidei as a separate superfamily, Lepidogalaxioidea, along with the Esocoidea (Esocidae + Umbridae). The Esocoidea are restricted to the northern part of the Northern Hemisphere. Fink & Weitzman (1982) were not convinced that *Lepidogalaxias* was an esocoid and recommended further study. Roberts (1984) hypothesised that *Lepidogalaxias* might be a highly specialised galaxiid or galaxioid derivative. Emphasising its uniqueness and uncertain phylogenetic position, in 1984 Nelson placed *Lepidogalaxias* in its own suborder, the Lepidogalaxioidei, within the order Salmoniformes (with the Esocoidei, Argentinoidei, and Salmonoidei).

McDowall & Pusey (1983) provided a new description of *Lepidogalaxias*, briefly reviewed the controversy, but provided no new evidence concerning its relationships. Fink (1984) was also unconvinced of Rosen's (1974) hypothesis that *Lepidogalaxias* is an esocoid, and using new characters, placed it, the Salmonidae, and the Neoteleostei in an unresolved trichotomy. He noted, however, that (p. 205) "more work remains to be done before we can be really confident in [its] phylogenetic placement." Apparently because of the uncertainty, Rosen (1985) excluded *Lepidogalaxias* from his cladogram of clupeocephalan relationships, and stated only that evidence supporting either a neoteleost, galaxiid or esocoid relationship was available. More recently, Begle (1991) presented a cladistic analysis of the lower euteleosts. He hypothesised that *Lepidogalaxias* is the sister group of a clade made up of (Salangidae + [*Lovettia* + (*Aplochiton* + Galaxiidae)]) and that Retropinnidae + Prototroctidae is the sister group of these five taxa. In Nelson's (1994) current classification *Lepidogalaxias* is placed in its own family, Lepidogalaxiidae, within superfamily Galaxioidea of the suborder Osmeroidei (with superfamily Osmeroidea) within the order Osmeriformes (with suborder Argentinoidei). Most recently, Johnson & Patterson (1995, 1996) hypothesise that *Aplochiton* and Galaxiidae are sister taxa, that *Lovettia* and *Lepidogalaxias* are sister taxa, and that the sister group of these two clades is the Retropinnidae (*Retropinna* + *Stokellia* + *Prototroctes*).

I examined the galaxioids and *Lepidogalaxias* as part of a comprehensive study of the suspensorium and its muscles in the salmoniforms and their relatives (Williams, 1987). This study yielded considerable new osteological and myological information. Some of this information constitutes evidence bearing on galaxioid intrarelationships and the phylogenetic position of *Lepidogalaxias*. In the present paper I describe in detail the suspensorium and its muscles in the galaxioids and *Lepidogalaxias*, and discuss the phylogenetic relationships that are suggested by the new data on bones and muscles of the suspensorium. The suggested phylogeny should not be considered definitive since it is based on data from a single character complex. Evidence from other anatomical systems as well as from other sources such as molecular sequences will have to be considered before a definitive hypothesis emerges. Nevertheless, the suspensorium provides critical new information potentially helpful for solving the riddle of galaxioid relationships.

Materials and methods

Specimens were cleared and stained for cartilage and bone using Taylor & Van Dyke's (1985) method. Radiographs of some fish were taken using a "Torrex 150 Radiographic-Fluoroscopic System." Dissections and drawings were made using a Wild M7A stereomicroscope equipped with a camera lucida. The standard length of each specimen was measured with Helios needle-pointed dial callipers. Osteological nomenclature follows Norden (1961) and Harder (1975). Muscle nomenclature follows Winterbottom (1974). The term tendon is frequently synonymised with ligament, not because they are difficult to distinguish, but because they are often homologous. The term endochondral refers to an ossification having a cartilaginous precursor. On cleared and stained specimens this is seen as a thickened bone (red) with a cartilaginous (blue) core. A dermal ossification does not arise from cartilage and is stained only red. The palatine has an endochondral component (the autopalatine) and a dermal component (the dermopalatine). The metapterygoid, quadrate, symplectic, and hyomandibular are endochondral but can have membranous laminae that are stained only red. The ectopterygoid, mesopterygoid, and preoperculum are dermal bones.

Unless noted, in the following text I use the name Salmoniformes in its traditional way (*sensu* Nelson, 1984) because of the prevalent usage of this name in

the literature, and because the relationships of its members are still controversial. In Nelson's (1994) new classification Salmoniformes refers only to the family Salmonidae. Otherwise names of taxa follow Nelson 1994 except that: Esocoidei = Esocidae + Umbridae; Salangidae = Salangidae + Sundasalangidae; osmeroids = Osmeridae (*Hypomesus* + *Mallotus* + *Allosmerus* + *Osmerus* + *Spirinchus* + *Thaleichthys* + *Plecoglossus*) + Salangidae; and Retropinnidae (*Retropinna* + *Stokellia*), Prototroctidae (*Prototroctes*), Galaxiidae, and Aplochitonidae (*Aplochiton* + *Lovettia*) are each *sensu* McDowall (1969). Contrary to Nelson (1994) I do not use the term Esociformes (= my Escoidei) nor Osmeriformes (= Argentinoidei + my osmeroids + my galaxioids which include *Lepidogalaxias*).

I evaluated galaxioid intrarelationships as part of a larger study involving all Salmoniformes (Williams, 1987). The cladistic relationships of galaxioids were studied using evidence from the bones and muscles of the suspensorium. Characters were selected, their states were documented, and outgroup analysis was used to decide polarity.

The traditional galaxioids (Retropinnidae + Prototroctidae + Galaxiidae + Aplochitonidae, all *sensu* McDowall, 1969) + *Lepidogalaxias* were considered to be the ingroup. Monophyly is supported by Williams (1987), Begle (1991), and Johnson & Patterson (1995, 1996). The monophyly of the galaxioids excluding *Lepidogalaxias* is supported by numerous earlier workers (e.g., McDowall, 1969, 1984; Nelson, 1970, 1972; Fink, 1984). These workers either did not examine *Lepidogalaxias*, placed it elsewhere, or considered its position uncertain. The monophyly of the Retropinnidae (*Retropinna* + *Stokellia*) is based on McDowall (1969, 1979, 1984) and Begle (1991). The Prototroctidae contains only *Prototroctes* (McDowall, 1969, 1976, 1984). There is substantial evidence that the family Galaxiidae itself is monophyletic (e.g., McDowall, 1969, 1984; Nelson, 1972; Rosen, 1974; Fink, 1984). Although McDowall (1969, 1971, 1984) expressed some uncertainty about monophyly of the Aplochitonidae, monophyly is supported by Williams (1996). However, some workers claim that the family is paraphyletic (Begle, 1991; Johnson & Patterson, 1995, 1996).

I examined several outgroups before deciding on the polarity of a character since the character states in the outgroup for a given set of characters are not necessarily primitive relative to the ingroup (Stiassny, 1986; Sanford, 1990). The first outgroup was the osmeroids. This choice is supported by numerous recent studies, including Fink & Weitzman (1982), Williams (1987), Sanford (1990), Begle (1991, 1992), Wilson & Williams (1991), and Johnson & Patterson (1995). More remote outgroups are problematical since there is no consensus of salmoniform intra- and interrelationships. However, based on Williams (1987), Fink & Weitzman (1982), Sanford (1990), and Begle (1991, 1992), the Argentinoidei are the second outgroup. Based on my larger study, the outgroup of the osmeroids + galaxioids + argentinoids is the Neoteleostei, and outgroups of these four taxa are the Ostariophysi and the Salmonidae + Esocoidei. I also studied representatives of other, phylogenetically more primitive teleostean taxa.

For most characters used all immediate outgroups had the same character state, judged to be primitive, and the polarity could be reliably estimated. In a few cases I used a character state as a synapomorphy if all the outgroups did not have the same state, but if the exception in the outgroups was restricted to a derived lineage. These exceptions are noted in the list of characters.

I also carried out a cladistic analysis using the branch-and-bound algorithm of PAUP 3.1.1. (Swofford, 1993). There were 21 characters with 26 apomorphic states. I treated all characters as unordered. Appendix 1 presents the input data matrix used in the numerical analysis.

Specimens from all the major salmoniform groups and the outgroups were examined. All taxa examined are listed in Appendix 2. The following museum acronyms are used on the figures: AMS—The Australian Museum, Sydney; CAS—California Academy of Sciences, San Francisco; NMC—National Museum of Natural Sciences, National Museums of Canada, Ottawa; UAMZ—The University of Alberta Museum of Zoology, Edmonton; WAM—Western Australian Museum, Perth. Other figure abbreviations are as follows: Aa—angulo-articular; AAP—adductor arcus palatini; A2—lateral section of adductor mandibulae; A2α, A2ß—subdivisions of section A2 of adductor mandibulae; A2.dm—dorsomedial subdivision of A2; Aw—section of adductor mandibulae filling Meckelian fossa; AO—adductor operculi; Bb.tp—basibranchial tooth-plate; Bh.tp—basihyal tooth-plate; Ch—ceratohyal; D—dentary; DO—dilatator operculi; Ec—ectopterygoid; E.lo—lamina orbitonasalis of ethmoid cartilage; Ep—epaxial muscles; E.pr—lateral prenasal process of ethmoid cartilage; Fr—frontal; Hh—hypohyal; Hm—hyomandibular; Hm.al—anterior lamina of hyomandibular; Hm.fl—lateral foramen for hyomandibular branch of facial nerve; Hm.fm—medial foramen for hyomandibular branch of facial nerve; Hm.h—head of hyomandibular; Hm.ls—lateral strut of hyomandibular; Hm.op—opercular arm of hyomandibular; Hm.v—ventral arm of hyomandibular; L—ligament; L.A2—tendon connecting section A2 of adductor mandibulae with angulo-articular in *Umbra limi* and *U. pygmaea*; L.cm—coronoid-maxilla ligament in Esocoidei; L.m—new ligament extending from maxilla to mandible in Aplochitonidae; L.mm—maxillo-mandibular ligament; L.smx—supramaxillary ligament; L.w, L.x, L.y, L.z—sections of maxillo-mandibular ligament; LAP—levator arcus palatini; Le—lateral ethmoid; LJ—lower jaw; LO—levator operculi; LO.p—posterior subdivision of levator operculi; md V—mandibular branch of trigeminal nerve; mm—millimetre(s); Ms—mesopterygoid; Ms.a—anterior end of mesopterygoid; Ms.t—mesopterygoidal teeth; Mt—metapterygoid; Mx—maxilla; Op—operculum; Pa—parietal; Pl—palatine; Pl.a—autopalatine; Pl.ac—anterior cartilage of autopalatine; Pl.d—dermopalatine; Pl-ec—fused palatine and ectopterygoid; Pmx—premaxilla; Po—preoperculum; Po.af—anterior flange of preoperculum; Po.al—anterior lamina of preoperculum; Po.d—dorsal limb of preoperculum; Po.v—ventral limb of

preoperculum; Pq—palatoquadrate cartilage; Pr—proethmoid; Pro—prootic; Pt—pterotic; Pts—pterosphenoid; Ptt—posttemporal; Q—quadrate; Q.b—body of quadrate; Q.c—condyle of quadrate; Q.j—quadratojugal arm of quadrate; Smx—supramaxilla; Sp—sphenotic; Sy—symplectic; Sy.l—lamina of symplectic; t.AM—tendinous aponeurosis extending to lower jaw.

Descriptions: bones of suspensorium

Palatine. The palatine and ectopterygoid are fused in *Retropinna* (Fig. 1). The area posterior to the last tooth is probably part of the original ectopterygoid since immediately behind this tooth the bone is slightly constricted, and the area posterior to this constriction is inclined at a slightly different angle. This part is also edentulous, flattened and blade-like, and overlaps the anterodorsal corner of the quadrate as in most salmoniforms. The area anterior to the central constriction is toothed and widens mediolaterally in an anterior direction to form a dorsally concave trough. The small autopalatine rests on its anterodorsal surface. The palatoquadrate cartilage emanating from the posterior end of the autopalatine is reduced. Unlike osmerids (Fig. 2), it does not extend dorsally to meet the lamina orbitonasalis of the ethmoid cartilage. The palatine and ectopterygoid are similar in *Prototroctes* (Fig. 3) except that the fused bone is straighter and the autopalatine is smaller, triangular and lacks an anterior cartilage. Unlike the other galaxioids, the palatine in *Lepidogalaxias* (Fig. 4) bears a row of teeth. The autopalatine and dermopalatine are fused. The cartilage at the anterior end of the palatine extends laterally as a finger-like hook that contacts the anteromedial surface of the maxilla. Salmonines have a similar hook. The lateral ethmoid contacts the dorsal surface of the cartilage at the anterior end of the palatine, unlike other salmoniforms. The palatoquadrate cartilage at the posterior end of the autopalatine is lost. The palatine in *Galaxias maculatus* lacks teeth and the dermopalatine is absent or greatly reduced (Fig. 5). The palatoquadrate cartilage at its posterior end is as in the Retropinnidae and Prototroctidae. The palatine is similar in other galaxiids (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974; Andrews, 1976). The palatine in *Aplochiton* resembles galaxiids but has an elongated anterior cartilage (Fig. 6). The palatine in *Lovettia* is poorly ossified, as are the other bones of the suspensorium.

Ectopterygoid. The palatine and ectopterygoid are fused in retropinnids and prototroctids (Figs 1, 3). The ectopterygoid in *Lepidogalaxias* is straight and short (Fig. 4). In galaxiids and aplochitonids it is absent and replaced by a ligament (Figs 5, 6: L). This ligament has never been described. Others have noted the absence of an ectopterygoid in these taxa, but none mention the ligament (e.g., Frankenberg, 1969; McDowall, 1969; Fink, 1984; Begle, 1991). A small, splint-like ectopterygoid is reported in *Lovettia* by McDowall (1969) and by G. David Johnson (personal communication); however, I did not observe this element as a separate ossification in my specimens.

Mesopterygoid. As in the Osmeridae (Fig. 2), the medioventral surface of the mesopterygoid in *Retropinna* (Fig. 1) bears a series of large, ventrolaterally curving teeth. In two specimens there were 30–40 teeth on each bone: a medial row of 15–20 teeth and 15–20 irregularly distributed lateral teeth. The teeth are largest medially and posteriorly. All retropinnids bear similar teeth (McDowall, 1979). The mesopterygoid in *Prototroctes* has more teeth (Fig. 3). *Lepidogalaxias* has a small, elliptical, edentulous mesopterygoid (Fig. 4). The mesopterygoid in *Galaxias maculatus* bears seven or eight ventroanterolaterally curving teeth in a single row along the anteromedial edge (Fig. 5). It is similar in other galaxiids except that teeth are few and sometimes absent in *Galaxias cleaveri* (Andrews, 1976; McDowall & Frankenberg, 1981) and in *Neochanna* (personal observation; McDowall, 1970). The mesopterygoid in *Aplochiton* resembles *Galaxias maculatus* but is longer (Fig. 6). It is similar in *Lovettia* but has only four or five teeth.

Quadrate. Quadrates in *Retropinna* and *Prototroctes* are similar (Figs 1, 3). The condyle and quadratojugal arm in *Lepidogalaxias* are unusually large (Fig. 4). *Galaxias maculatus* is similar (Fig. 5). Differences among galaxiids are minor. The quadrate in *Aplochiton* (Fig. 6) and *Lovettia* has a small body and a very long quadratojugal arm.

Symplectic. The symplectic in *Retropinna* and *Prototroctes* is distinctly bent and has a large cartilaginous knob at its anterior end (Figs 1, 3). *Lepidogalaxias* has a slightly bent symplectic (Fig. 4). In *Galaxias maculatus* its posterodorsal edge rests in a groove on the ventral edge of the metapterygoid (Fig. 5). Differences among galaxiids are minor (see also Frankenberg, 1969). The symplectic in *Aplochiton* (Fig. 6) and *Lovettia* does not contact the metapterygoid.

Metapterygoid. The metapterygoid in *Retropinna* and *Prototroctes* is endochondral except for a narrow membranous lamina extending along its dorsal edge (Figs 1, 3). Projecting from its posterodorsal corner is a large cartilage that abuts the middle of the lateral strut of the hyomandibular. The metapterygoid in *Lepidogalaxias* is small, axe-shaped, and entirely endochondral (Fig. 4). The metapterygoid in *Galaxias maculatus* has an anterior, axe-shaped endochondral section and a posterior, rounded membranous lamina (Fig. 5). Its ventral edge is tightly braced against both the symplectic and hyomandibular. The metapterygoid in other galaxiids is variable (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). *Neochanna* for example has a square metapterygoid with a reduced

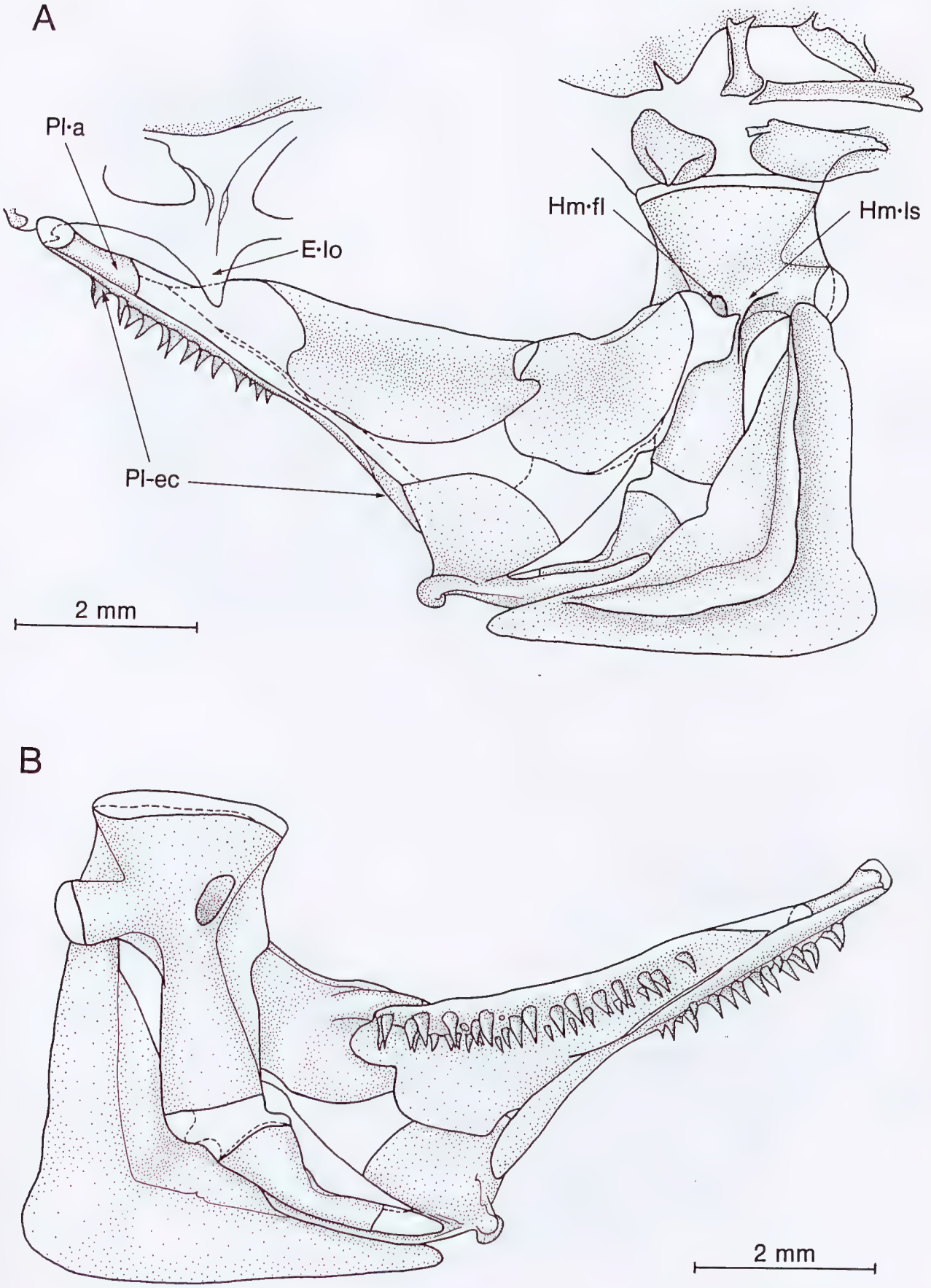

Fig. 1. Lateral (A) and medial (B) views of left suspensorium in *Retropinna retropinna* (UAMZ 4606, 71.5 mm). Stippling on Figs 1–6 and 17 indicates bone, while clear areas on and around bones bordered by lines indicate cartilage. Cartilaginous areas can be distinguished from bone by studying lateral and medial views.

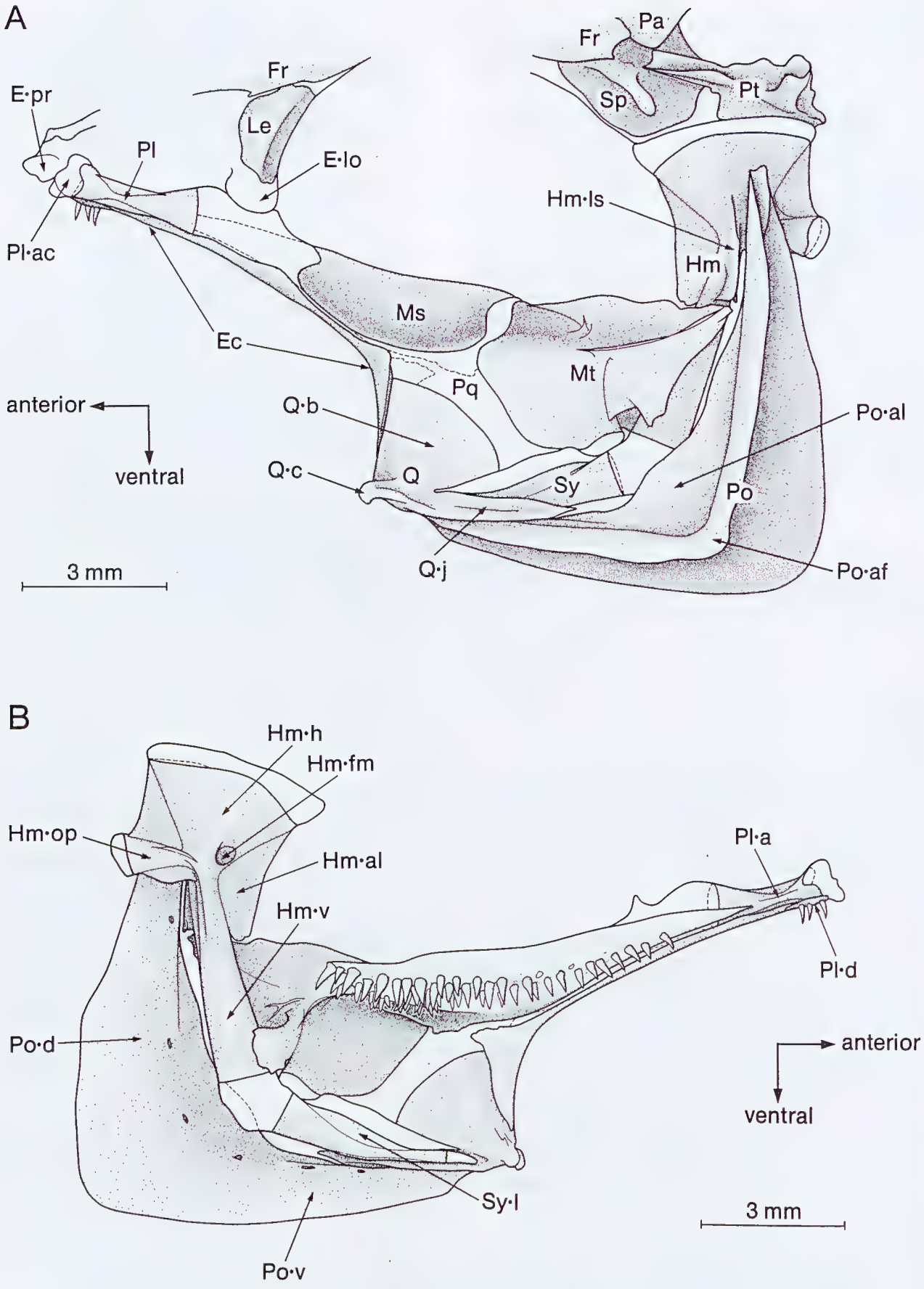

Fig. 2. Lateral (A) and medial (B) views of left suspensorium in *Hypomesus pretiosus* (UAMZ 874, 118.0 mm).

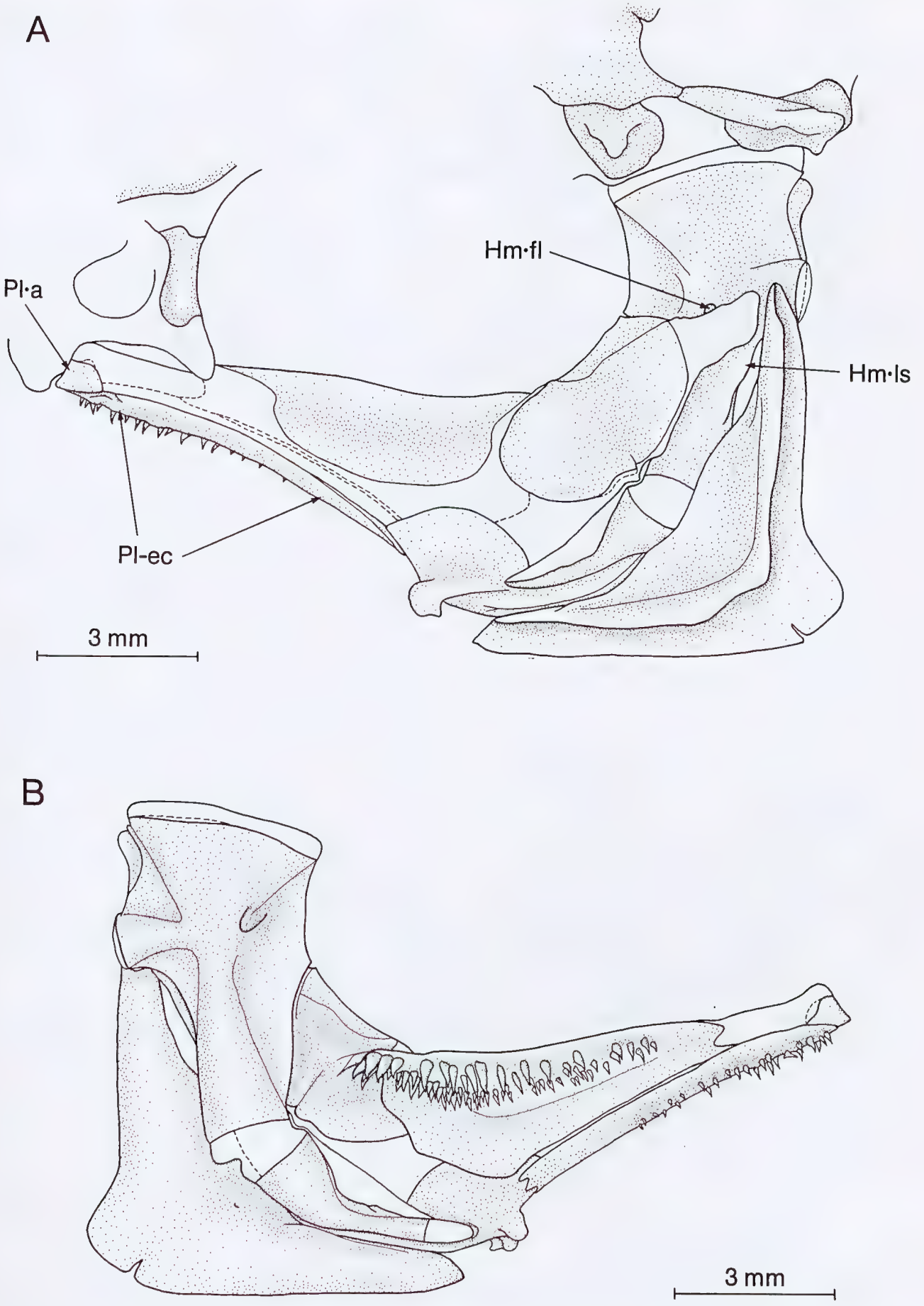

Fig. 3. Lateral (A) and medial (B) views of left suspensorium in *Prototroctes maraena* (UAMZ 6325, 117.0 mm).

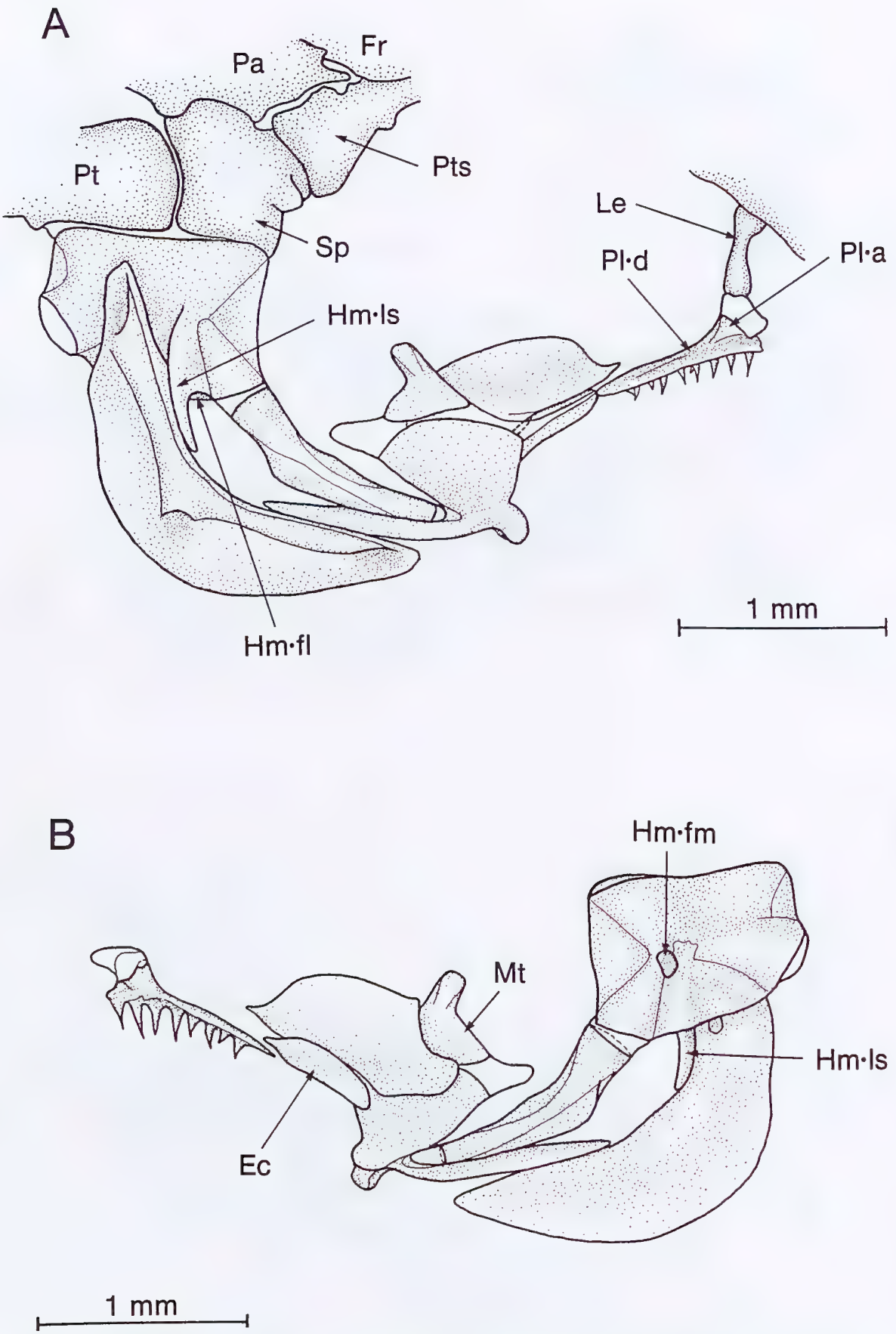

Fig. 4. Lateral (A) and medial (B) views of right suspensorium in *Lepidogalaxias salamandroides* (WAM P. 7578–81, 34.6 mm).

lamina. In *G. brevipinnis* the endochondral portion is small while the lamina is large. The metapterygoid in *G. paucispondylus* is widely separated from the mesopterygoid and quadrate and does not contact the hyomandibular; a feature shared with *Galaxiella pusilla* and *G. nigrostriata* (Frankenberg, 1969). The metapterygoid in *Aplochiton* (Fig. 6) and *Lovettia* is small, with a posteriorly extending finger-like projection, and is posterodorsal to the body of the quadrate.

Hyomandibular. The hyomandibular in *Retropinna* and *Prototroctes* is deeper than it is wide (Figs 1, 3). The small lateral strut is convex anteriorly as it arches posterodorsally from the ventral arm to the opercular arm (Fig. 1A: Hm.ls). The lateral foramen for the hyomandibular branch of the facial nerve is anterior to the middle of the lateral strut (Figs 1, 3: Hm.fl). The hyomandibular in *Lepidogalaxias* is wider than it is deep (Fig. 4). The ventral arm is very short. A vertical lateral strut (Fig. 4: Hm.ls) abuts the preoperculum. The lateral foramen (Fig. 4: Hm.fl) is on the mid-ventral edge of the hyomandibular at the ventral end of the lateral strut. The hyomandibular in *Galaxias maculatus* is about as wide as it is deep (Fig. 5). A wide, shelf-like lateral strut (Fig. 5A: Hm.ls) arches posterodorsally from the ventral arm to the opercular arm. The lateral foramen (Fig. 5A: Hm.fl) is posterior to the ventral end of the lateral strut. The hyomandibular in the other galaxiids is moderately variable (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). For example, in *Neochanna* and *G. brevipinnis* it is wider than in *G. maculatus* and has a shorter ventral arm. The lateral strut in *G. paucispondylus* and *Brachygalaxias* is larger than in the other species examined. The lateral foramen in *Neochanna* is at the ventral end of the lateral strut. The hyomandibular in *Aplochiton* is deeper than it is wide (Fig. 6). The lateral strut resembles galaxiids but is less robust (Fig. 6: Hm.ls). The lateral foramen (Fig. 6: Hm.fl) is anterior to the ventral end of the lateral strut. The hyomandibular in *Lovettia* is about as wide as it is deep. The ventral arm is shorter than in *Aplochiton* and only slightly expanded ventrally. Although a lateral strut is absent the lateral foramen occupies the same position.

Preoperculum. In *Retropinna* the ventral limb of the preoperculum is longer than the dorsal limb (Fig. 1). The lateral sensory canal is completely open posterior to a flange that runs along the entire length of the anterolateral surface of the preoperculum. *Retropinna* lacks a suprapreoperculum (like all galaxioids). The preoperculum in the Prototroctidae, Galaxiidae, and Aplochitonidae resembles *Retropinna* (Figs 3, 5, 6; see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). *Lepidogalaxias* has dorsal and ventral limbs of equal length (Fig. 4). A bone-enclosed lateral sensory canal runs the length of its anterior surface and gives off three pores, one at each end of the bone, and one at the intersection of the two limbs.

Descriptions: muscles of suspensorium

Adductor mandibulae. The adductor mandibulae in *Retropinna* has a posterior A2 section and an anterior Aw section (Fig. 7). The mandibular branch of the trigeminal nerve (Fig. 7: md V) passes lateral to the anterodorsal end of the adductor mandibulae at the division of A2 and Aw before running lateral to Aw and then medial to the lower jaw. Section A2 originates from the preoperculum, hyomandibular, metapterygoid, symplectic, and quadrate. The medial fibres insert on the lateral surface of a tendinous aponeurosis (Fig. 7: t.AM) that overlies the quadrate and metapterygoid. This aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer dorsal tendon attaching farther anteriorly along and next to Meckel's cartilage. Section Aw fills the Meckelian fossa on the medial side of the lower jaw. It originates primarily from the dorsal tendon (anterior to A2) and inserts onto the dorsal border of Meckel's cartilage and the angulo-articular and dentary. The dorsolateral fibres of A2 converge onto a flattened tendon that extends anteriorly to join the posterodorsal part of the maxillo-mandibular ligament (Fig. 7: L.mm). This tendon is continuous with the dorsal part of the tendinous aponeurosis. The maxillo-mandibular ligament extends from the angulo-articular to the maxilla. Like all galaxioids there are no supramaxillae. *Prototroctes* (Fig. 8) has a similar adductor mandibulae except that ligament L.mm is shorter. The mandibular branch of the trigeminal nerve also passes medial to the anterior end of the adductor mandibulae before running medial to the lower jaw, a feature shared with *Lepidogalaxias*, galaxiids, and aplochitonids.

The adductor mandibulae in *Lepidogalaxias* extends unusually far dorsally, originating from the levator arcus palatini, dilatator operculi, hyomandibular, symplectic, and quadrate (Fig. 9). The medial fibres of A2 insert onto a long, flat, narrow tendinous aponeurosis that overlies the quadrate and extends anteriorly medial to the lower jaw to attach to the coronomeckelian. This aponeurosis does not bifurcate anteriorly. There is no Aw. The lateral fibres of A2 insert tendinously on both the maxilla and lower jaw. They converge anteriorly to fit into a tendinous "glove" that opens posteriorly. The glove, in turn, inserts onto the medial and lateral surfaces of the coronoid process (dentary) of the lower jaw. Extending anteriorly from the anterodorsal part of the tendinous "glove" is a short, flattened tendon that inserts onto the dorsal edge of the posterior third of the maxilla. This tendon and "glove" are not continuous with the aponeurosis extending to the coronomeckelian. A short ligament (Fig. 9: L) joins the posteromedial surface of the maxilla with the coronoid process anterior to the insertion of the adductor mandibulae. It is also present in galaxiids and aplochitonids.

In *Galaxias maculatus* the adductor mandibulae has an A2 section that originates from the preoperculum, metapterygoid, hyomandibular, symplectic, and quadrate (Fig. 10). It has a small dorsomedial subdivision that

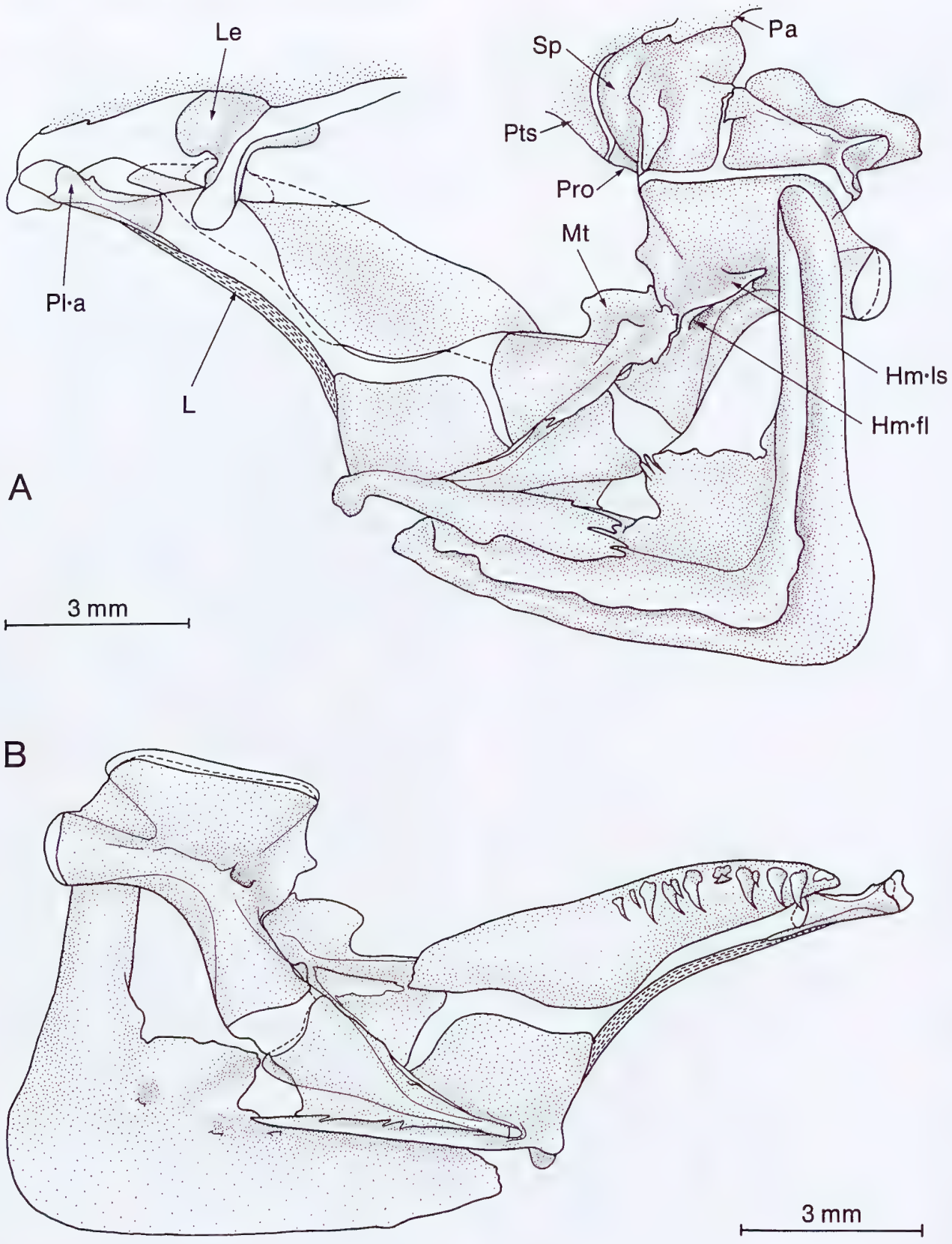

Fig. 5. Lateral (A) and medial (B) views of left suspensorium in *Galaxias maculatus* (UAMZ 4609, 117.9 mm).

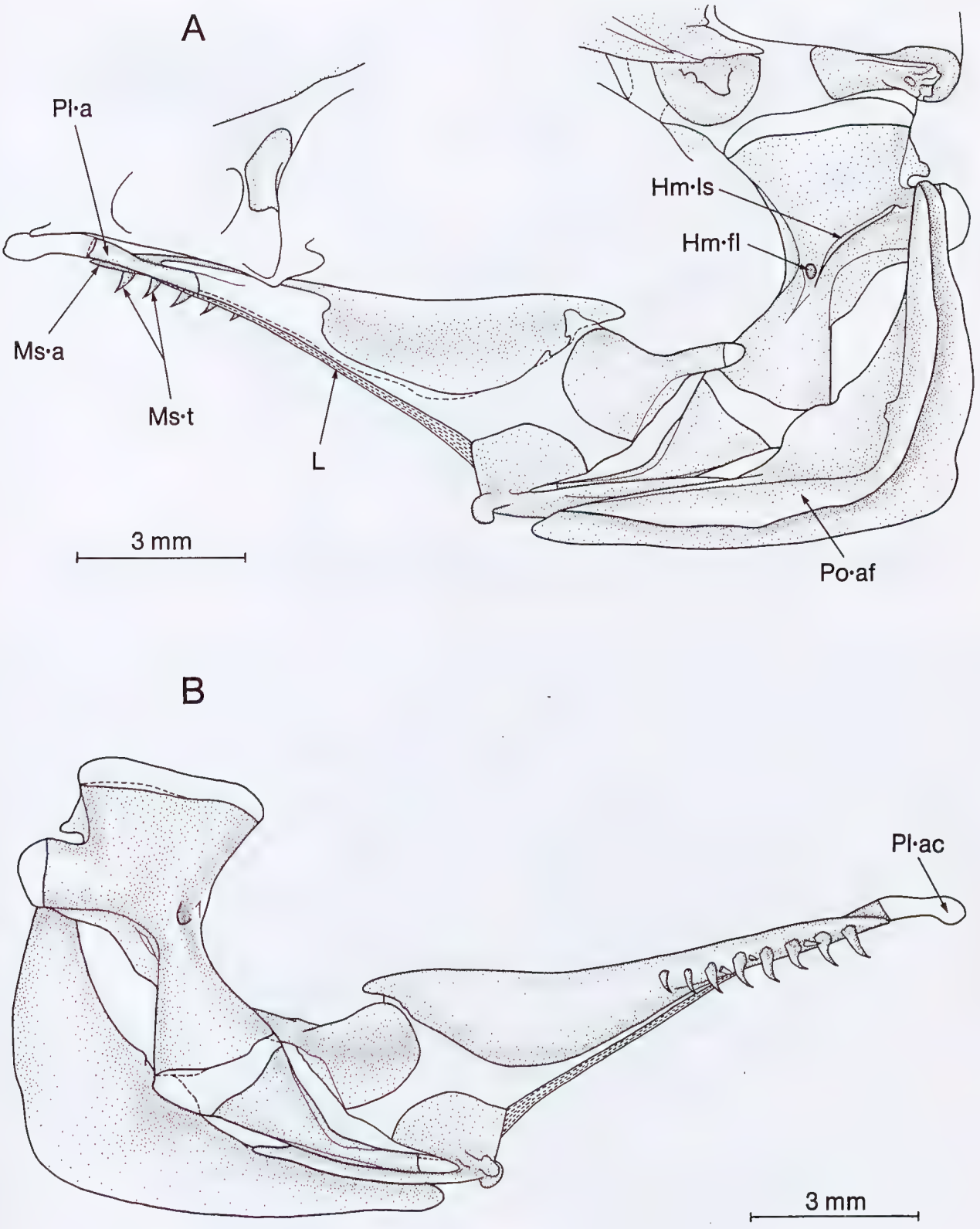

Fig. 6. Lateral (A) and medial (B) views of left suspensorium in *Aplochiton taeniatus* (NMC 76-0393, 110.5 mm).

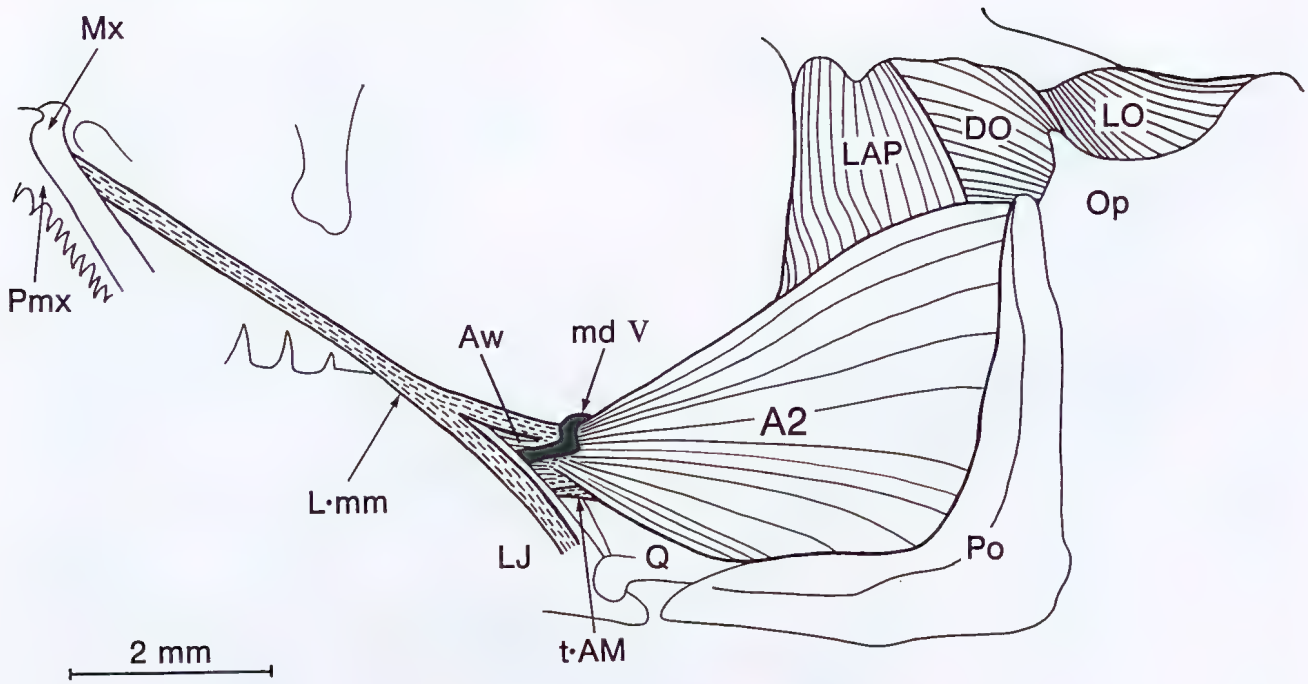

Fig. 7. Lateral view of external muscles of left suspensorium in *Retropinna retropinna* (UAMZ 4606, 77.0 mm). On Figs 7–12, 14–16, 18, and 19 muscles are indicated by closely spaced parallel lines; ligaments and tendons are short, closely spaced dashes; bones are outlined or stippled.

passes medial to the levator arcus palatini and originates from the metapterygoid. Its anteroventral fibres are continuous with those of A2. The medial and posterodorsal fibres of A2 (including the subdivision) insert on a tendinous aponeurosis similar to that in *Lepidogalaxias* except that it bifurcates when passing medial to the lower jaw: the ventral tendon attaches to the coronomeckelian and the longer, narrower dorsal tendon attaches to Meckel's cartilage and the angulo-articular. An Aw section fills the Meckelian fossa. It originates from the dorsal tendon of the aponeurosis and inserts on the dorsomedial surface of the lower jaw. The fibres of A2 converge on a flattened tendon that extends anteriorly to the dorsolateral surface of the middle of the maxilla. Removing the anterolateral fibres of A2 reveals a unique tendinous arrangement attaching A2 to the lower jaw (see Fig. 10B). A short and narrow tendon (L.y) extends ventrally from the posteriormost end of tendon L.x to the angulo-articular. Another narrow tendon (L.w) extends anteroventrally from the intersection of tendons L.x and L.y to the coronoid process (dentary) of the lower jaw. The adductor mandibulae in other galaxiids is similar to *Galaxias maculatus* but can differ in relative size, shape, and length and degree of development of the tendons connecting it to the upper and lower jaws. In *G. fasciatus* (Fig. 11), *G. brevipinnis* and *Neochanna* it is shorter anteroposteriorly and thicker than in the other galaxiids. The very large adductor mandibulae in *Neochanna* entirely covers the levator arcus palatini and dilatator operculi. Tendon L.x is longest and inserted farthest anteriorly in *G. maculatus*. In *G. paucispondylus*, and *Neochanna* L.x is short but broad, and inserts about a third of the way from the posterior end of the maxilla. It is longer in *Brachygalaxias, G. brevipinnis*, and *G. fasciatus* and inserts farther anteriorly. Tendon L.y in *Brachygalaxias, G. paucispondylus, G. brevipinnis*, and *G. fasciatus* is similar to *G. maculatus*. Tendon L.w. is variable and in some species resembles the tendinous "glove" in *Lepidogalaxias*. In *G. paucispondylus* L.w is broader and shorter than in *G. maculatus*. In *Brachygalaxias, G. brevipinnis*, and *G. fasciatus* (Fig. 11B: L.w) it is even shorter and forms a tendinous sheath that inserts broadly on the coronoid process. In *Neochanna* this broad sheath extends ventrally to both angulo-articular and dentary. A vestige of tendon L.y was present at the posteroventral corner of the sheath on one side of each specimen.

The adductor mandibulae in *Aplochiton* (Fig. 12) resembles *Galaxias maculatus* but is thinner and does not extend as far anteriorly. There is a partial dorsomedial subdivision whose dorsolateral fibres are separable from the main muscle. The subdivision does not pass medial to the levator arcus palatini. Section Aw is also larger. Section L.x is longer, L.w is thinner, and the posterodorsal corner of L.x is barely continuous with the aponeurosis that extends medial to the lower jaw. *Aplochiton* has a separate ligament (Fig. 12: L.m) extending from the ventral end of L.y to the anterior end of L.x of the maxillo-mandibular ligament. The adductor mandibulae in *Lovettia* resembles *Aplochiton* but there may not be a partial dorsomedial subdivision of A2, and I am uncertain whether the posteriormost end of the tendon extending from the adductor mandibulae to the maxilla joins the tendinous aponeurosis. It has ligament L.m.

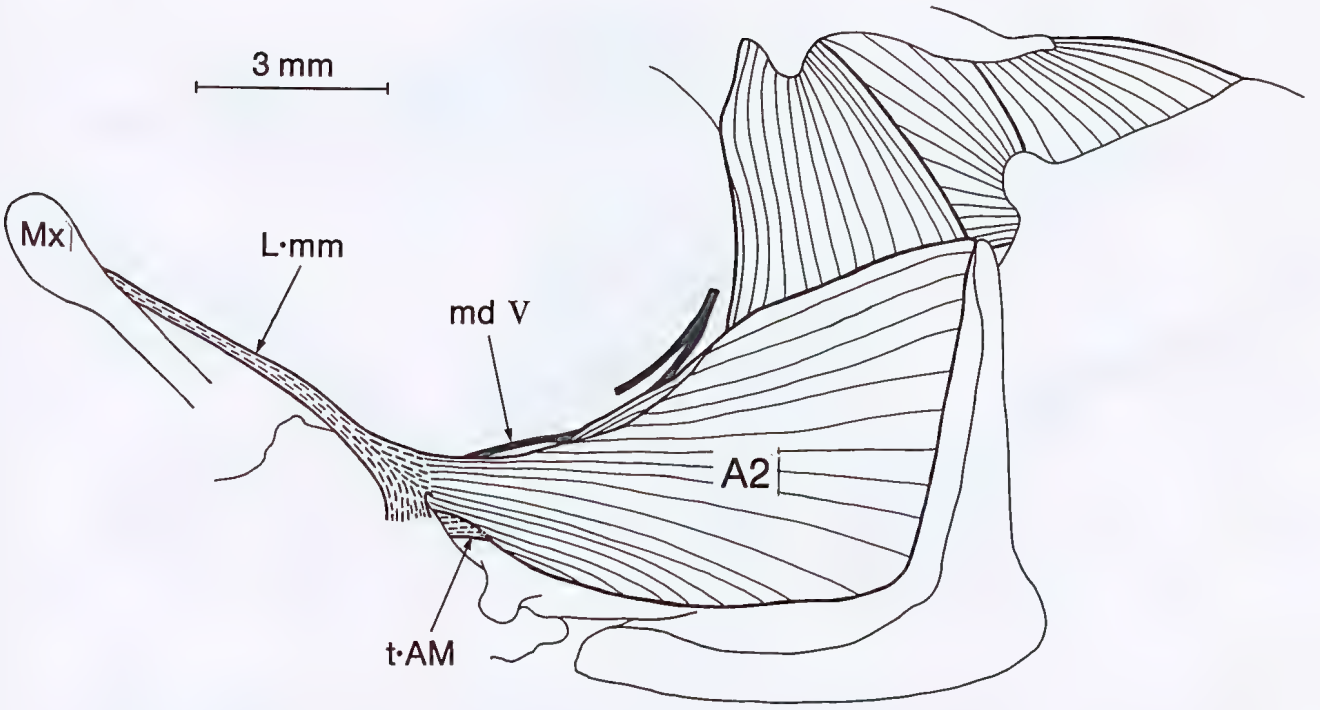

Fig. 8. Lateral view of external muscles of left suspensorium in *Prototroctes maraena* (UAMZ 6325, 122.1 mm).

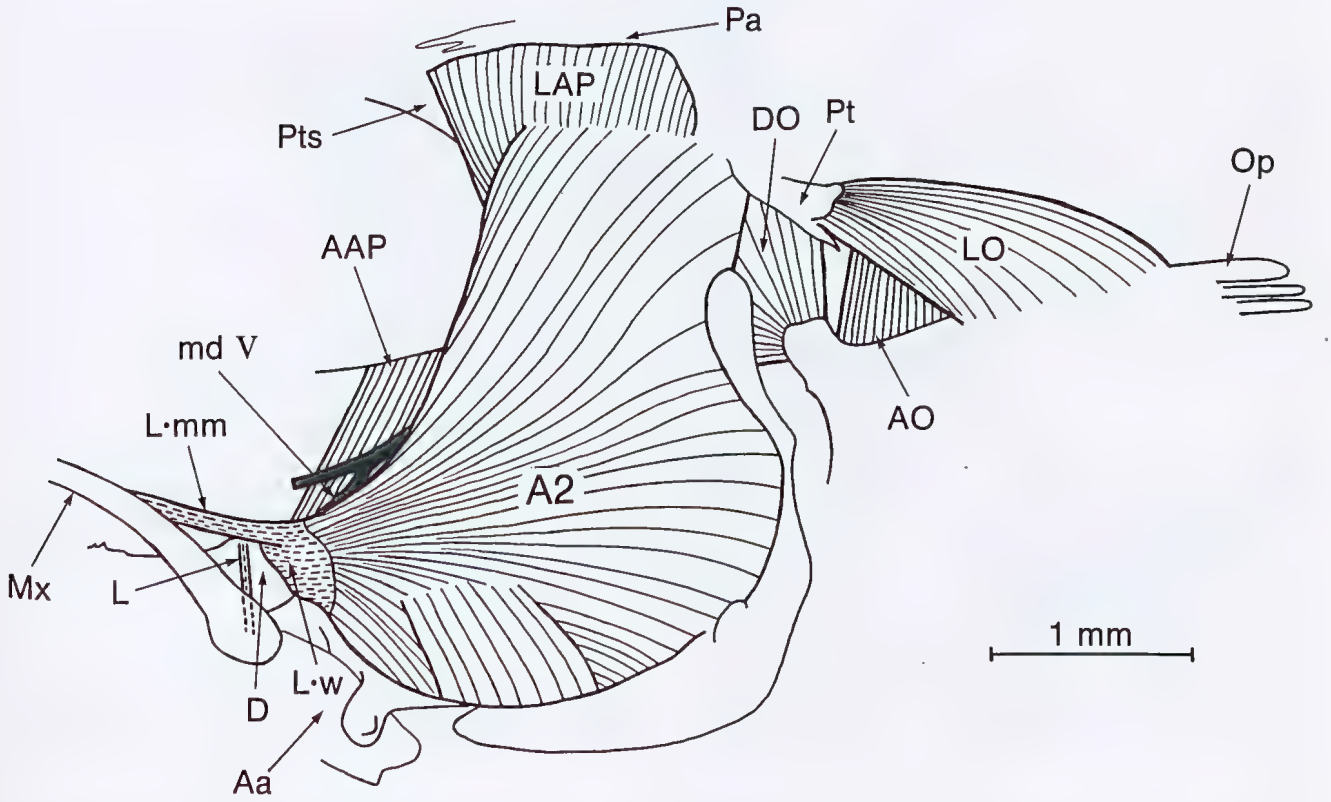

Fig. 9. Lateral view of external muscles of left suspensorium in *Lepidogalaxias salamandroides* (WAM P. 8124–31, 39.7 mm).

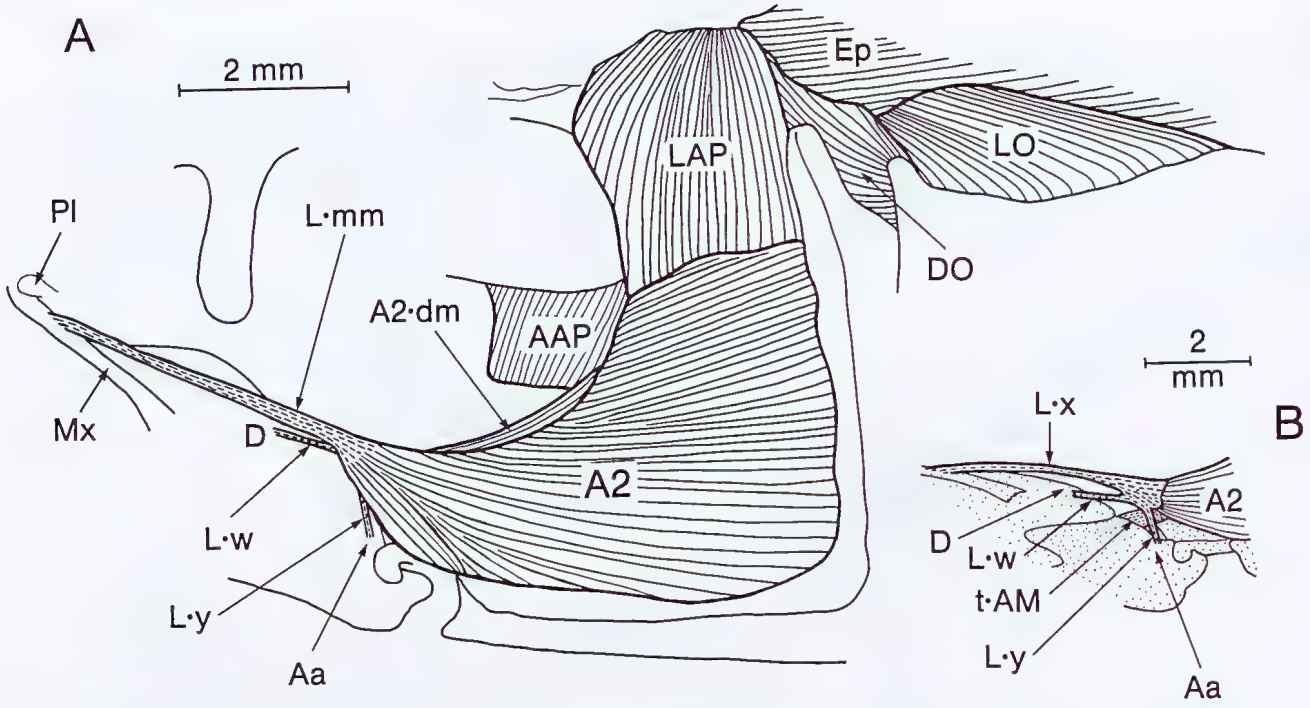

Fig. 10. *Galaxias maculatus* (UAMZ 4609, 92.6 mm): (A) lateral view of external muscles of left suspensorium; (B) ventrolateral (slightly posterior) view of tendons/ligaments attaching section A2 of adductor mandibulae onto maxilla and lower jaw, anterolateral fibres of section A2 inserting onto tendons/ligaments are removed. Ligament L (see Fig. 9) is not drawn.

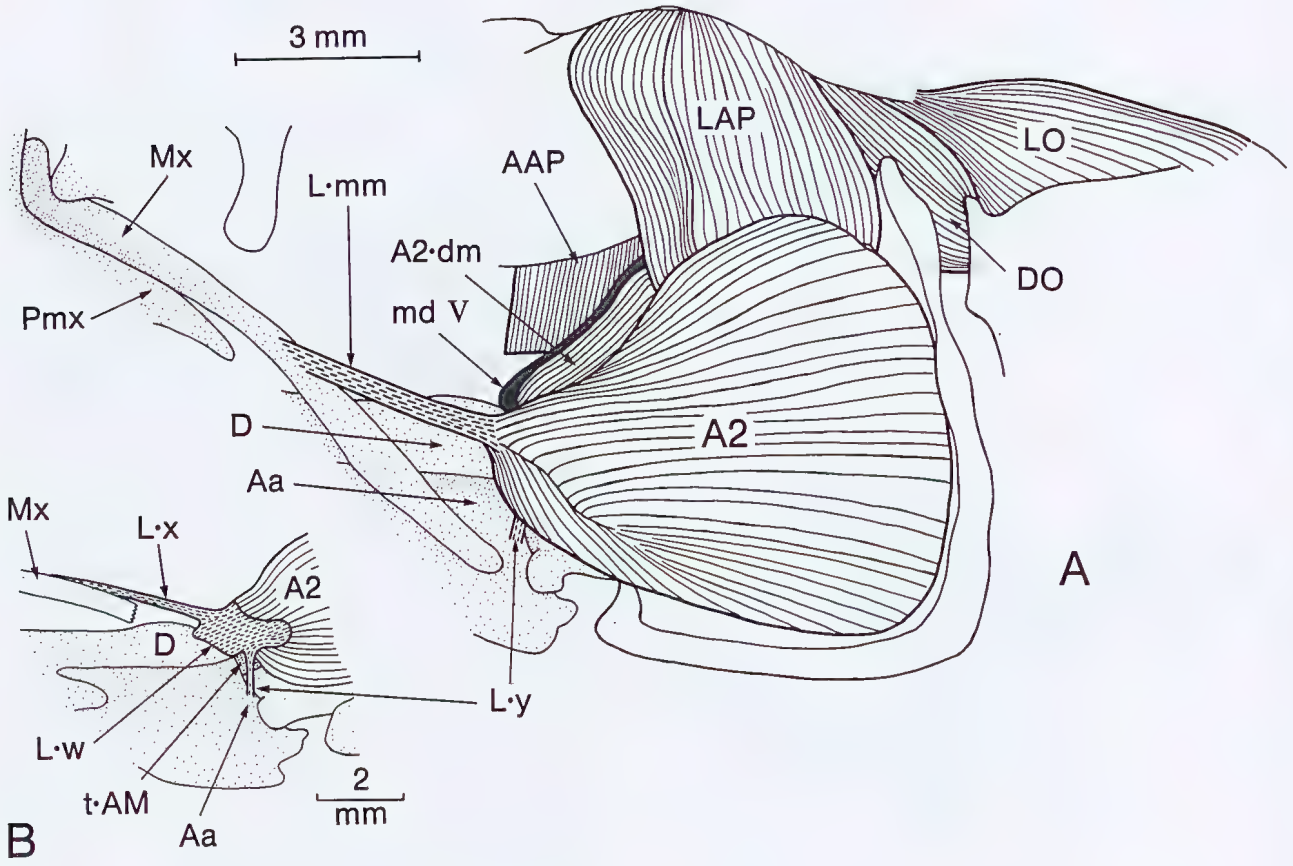

Fig. 11. *Galaxias fasciatus* (UAMZ 5122, 95.2 mm): (A) lateral view of external muscles of left suspensorium; (B) ventrolateral (slightly posterior) view of tendons/ligaments attaching section A2 of adductor mandibulae onto maxilla and lower jaw, anterolateral fibres of section A2 inserting onto tendons/ligaments are removed. Ligament L (see Fig. 9) is not drawn.

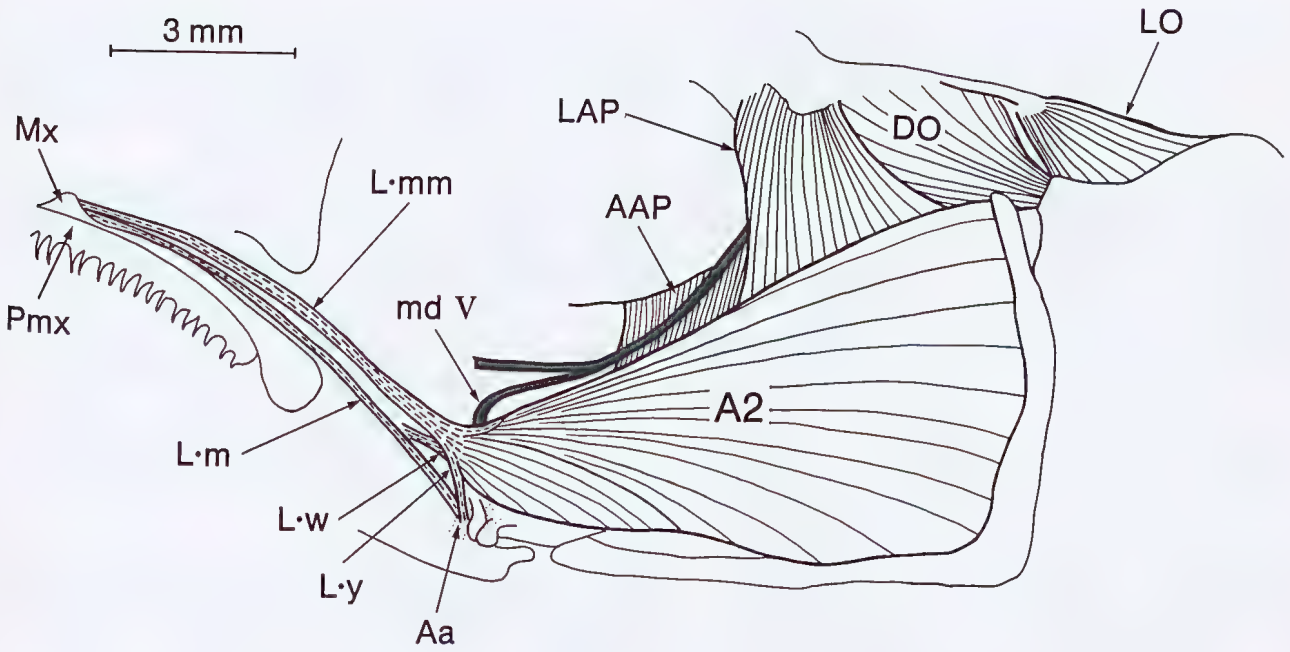

Fig. 12. Lateral view of external muscles of left suspensorium in *Aplochiton taeniatus* (NMC 76-0393, 104.1 mm). Ligament L (see Fig. 9) is not drawn.

Levator arcus palatini. The levator arcus palatini (LAP) in *Retropinna* and *Prototroctes* is conical and slightly bulbous (Figs 7, 8). It originates from the sphenotic and inserts on the hyomandibular and metapterygoid. The LAP in *Lepidogalaxias* is barrel-shaped and mostly covered by the adductor mandibulae (Fig. 9). It originates from the pterosphenoid, sphenotic, frontal, parietal, and possibly the prootic and pterotic. It inserts on the hyomandibular, symplectic, and palatoquadrate cartilage. The LAP in *Galaxias maculatus* (Fig. 10), *G. paucispondylus, G. brevipinnis*, and *G. fasciatus* (Fig. 11) resembles *Lepidogalaxias* except the origin excludes the pterotic and the insertion is on the hyomandibular and metapterygoid. In *Neochanna* it is covered by the greatly enlarged adductor mandibulae and has a broad area of origin primarily along the edges of the frontal and pterosphenoid. The LAP in *Brachygalaxias* is smaller than in the other galaxiids, conical, and not expanded dorsally onto the skull (the origin includes only the sphenotic). The LAP in *Aplochiton* resembles *Retropinna* (Fig. 12). It is similar in *Lovettia* except that the insertion includes the symplectic, not the metapterygoid.

Dilatator operculi. The conical dilatator operculi (DO) in *Retropinna* (Fig. 7) originates from the head of the hyomandibular, sphenotic, and pterotic, and inserts broadly on the articular process of the operculum. It is similar in other galaxioids (Figs 8–12).

Levator operculi. The flattened, fan-shaped levator operculi (LO) in *Retropinna* and *Prototroctes* (Figs 7, 8) originates from the pterotic and inserts on the dorsal third to quarter of the medial surface of the operculum. The LO in *Lepidogalaxias* is slightly bulbous, fan-shaped, and originates from the pterotic (Fig. 9). Unlike other galaxioids, it inserts only along the dorsal edge of the operculum (mostly along the dorsomedial edge but with the lateralmost fibres extending onto the dorsolateral surface). The LO in *Galaxias maculatus* is similar to *Lepidogalaxias* but inserts on the dorsal third of the medial surface of the operculum (Fig. 10). The LO in *G. brevipinnis, G. paucispondylus, G. fasciatus* (Fig. 11), and *Brachygalaxias* resembles *G. maculatus* except that its insertion covers a greater opercular surface. In *Neochanna* it covers the dorsal two-thirds of both sides of the operculum. The LO in *Aplochiton* and *Lovettia* is smaller than in galaxiids, and inserts onto only the dorsal quarter of the medial surface of the operculum (Fig. 12).

Adductor operculi. The adductor operculi (AO) in *Retropinna* and *Prototroctes* is conical to cylindrical, and completely covered by the anterior part of the LO. It originates from the pterotic and exoccipital medioventral to the origin of the LO and inserts on the medial surface of the anterodorsal corner of the operculum. The insertion is slightly ventral to the insertion of the anterior part of the LO, and lies medial to it. The AO in *Lepidogalaxias* is partly visible externally (Fig. 9). In galaxiids and aplochitonids it originates only from the pterotic.

Adductor arcus palatini. The adductor arcus palatini (AAP) in *Retropinna* and *Prototroctes* is flattened and rectangular. It originates primarily from the prootic and

inserts on the dorsomedial surface of the metapterygoid and on the medial surface of the hyomandibular. Next to its posterior end is an adductor hyomandibulae (AH) that originates on the pterotic and inserts along the dorsomedial edge of the opercular arm of the hyomandibular. The AAP in *Lepidogalaxias* is longer anteroposteriorly than in *Retropinna* and *Prototroctes* (Fig. 9). It originates from the parasphenoid, prootic, and pterotic. The insertion includes most of the medial surface of the hyomandibular, the dorsomedial edge of the palatoquadrate cartilage posterior to the metapterygoid, the lateral surface of the metapterygoid, and the posterodorsal surface of the mesopterygoid. The AAP in galaxiids is similar except the insertion includes less of the hyomandibular, does not include the palatoquadrate cartilage, and is from the medial surface of the metapterygoid (Figs 10, 11). The AAP in *Aplochiton* resembles the galaxiids (Fig. 12). The AAP in *Lovettia* resembles *Aplochiton* except that the insertion is as in *Lepidogalaxias*. Aplochitonids, galaxiids, and *Lepidogalaxias* lack an AH (I did not check *Brachygalaxias*).

Hypothesis of galaxioid intrarelationships

Figure 13 presents the galaxioid relationships suggested by the data from the suspensorium and its muscles. The branch-and-bound algorithm of PAUP, which guarantees the most parsimonious tree(s), revealed a single shortest tree. The PAUP analysis included 21 characters with 26 apomorphic states. Since the most parsimonious tree had 27 steps only one character was incompatible (character 6), and the consistency index was 0.963.

What follows is a discussion of the synapomorphies supporting each clade. For each description the derived states are presented first, followed by taxa sharing this state if it is not unique, followed by the primitive state.

Galaxioids (Retropinnidae + Prototroctidae + *Lepidogalaxias* + Galaxiidae + Aplochitonidae)

(1) *Autopalatine small* (shared with most Salmonidae, *Dallia*, and *Umbra*). Primitively, it is somewhat large with expanded ends.

(2) *Palatoquadrate cartilage at posterior end of autopalatine reduced or absent.* Primitively it expands dorsally towards the lamina orbitonasalis.

(3) *Ventral limb of preoperculum as long as, or longer than, dorsal limb* (shared with *Dallia*, Salangidae, and Argentinoidea). Primitively, the dorsal limb is longer than the ventral limb.

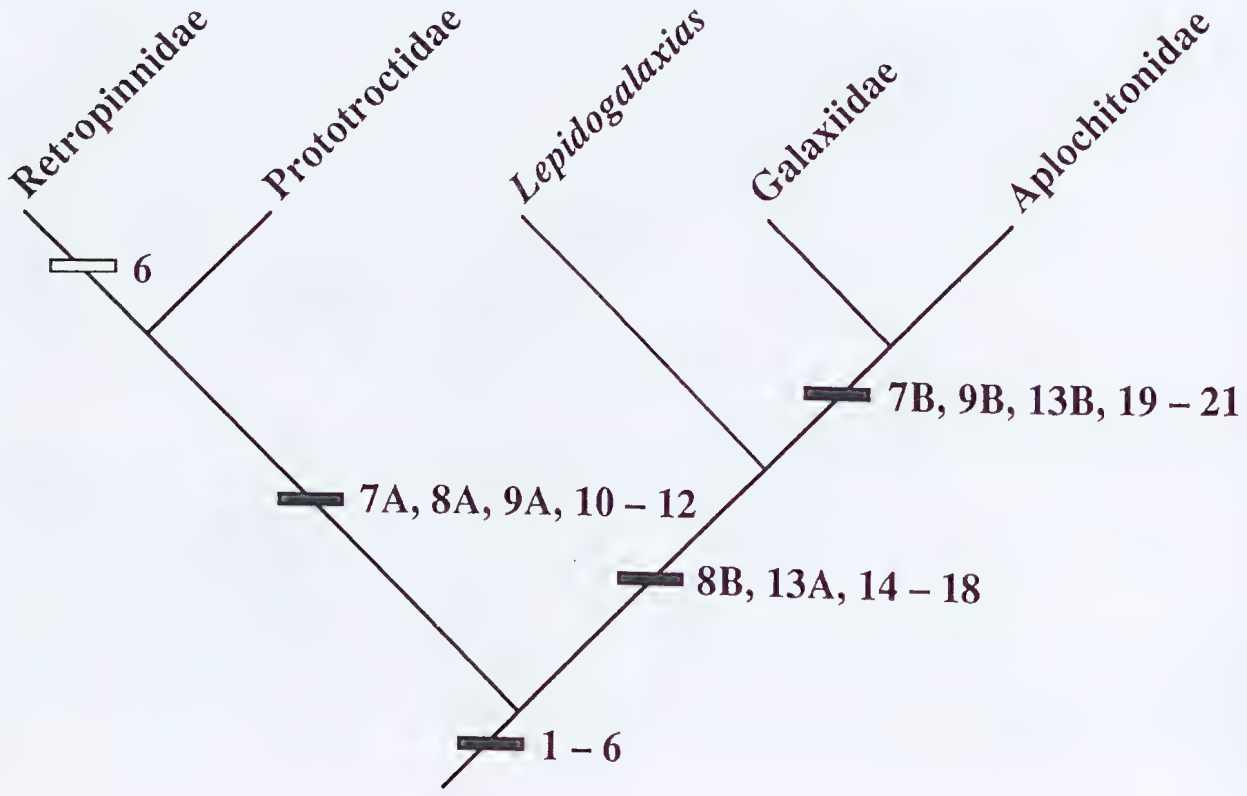

Fig. 13. Galaxioid relationships suggested by the suspensorium and its muscles. Synapomorphies correspond to those discussed in the text. The open bar indicates character 6 in its reversed state.

(4) *Supramaxillae and supramaxillary ligament absent* (shared with adult *Plecoglossus*, some Salangidae, and Argentinoidea). Primitively in Teleostei there are two supramaxillae, and a supramaxillary ligament extends from the anterior tip of the posterior one to the lower jaw.

(5) *Origin of adductor mandibulae includes most of lateral surface of preoperculum anterior to lateral sensory canal* (shared with Esocoidei and Argentinoidea). Primitively, the adductor mandibulae originates only along the anterolateral edge of the preoperculum.

(6) *Mandibular branch of trigeminal nerve passes medial to anterior end of section A2 of adductor mandibulae before running medial to lower jaw* (shared with Argentinidae and Bathylagidae). The assumption is that a reversal has occurred in *Retropinna* since it has the primitive state. Primitively, the nerve passes lateral to the anterior end of section A2 before running medial to the lower jaw (e.g., Figs 7, 14). Most lower teleosts (e.g., *Chanos, Clupea, Hiodon, Elops*) and primitive neoteleosts (e.g., *Diplophos, Vinciguerria, Aulopus*) have this state. Although the nerve technically passes medial to the anterior end of section A2 in *Umbra limi* and *U. pygmaea* this is related to a feature uniting them: the anterolateral fibres of section A2 converge onto a unique tendon (Fig. 15: L.A2) extending to the angulo-articular. The nerve rests lateral to the anterior end of section A2 at the division of sections A2 and Aw, as in all other esocoids, but is medial to the new tendon and the anterolateral fibres of section A2 that converge onto it. Hence it occupies the same relative position as the other esocoids and is the primitive state (compare Fig. 15 of *U. limi* with Fig. 16 of *U. krameri*, the sister species of *U. limi* + *U. pygmaea*; Wilson & Veilleux, 1982).

Retropinnidae + Prototroctidae

(7) *Ectopterygoid fused with palatine* (Fig. 13: 7A). *Dallia* questionably shares this state. It can be argued that in *Dallia* the ectopterygoid is lost, and the dermopalatine is greatly expanded posteriorly to nearly touch the anterodorsal corner of the quadrate (see also Wilson & Veilleux, 1982). However, even if the ectopterygoid and palatine are fused in *Dallia*, the so-called fused bone is unlike the one in the Retropinnidae and Prototroctidae because it is more robust, the teeth are larger and more numerous, and its posterior end does not overlap the quadrate. Primitively, palatine and ectopterygoid are separate. Galaxiidae and Aplochitonidae are united because they share an ectopterygoid that is greatly reduced or absent and largely or completely replaced by a prominent ligament (Fig. 13: 7B).

(8) *Lateral foramen for hyomandibular branch of facial nerve anterior to middle of lateral strut of hyomandibular* (Fig. 13: 8A). A lateral foramen at the ventral end of the lateral strut unites *Lepidogalaxias*, Galaxiidae, and Aplochitonidae (Fig. 13: 8B). A lateral strut is absent in *Lovettia*. Primitively, it is posterior to the dorsal half of the strut (see also Williams, 1987).

(9) *Lateral strut of hyomandibular convex anteriorly as it arches posterodorsally from ventral to opercular arm* (Fig. 13: 9A). A robust, shelf-like lateral strut, somewhat similar to the above, unites Galaxiidae and Aplochitonidae (Fig. 13: 9B). A lateral strut is absent in *Lovettia*. Primitively, the strut is concave anteriorly and inclined vertically between the ventral arm and the base of the head.

(10) *Large cartilage at posterodorsal corner of metapterygoid*. Primitively this cartilage is either small or lacking (usually).

(11) *Symplectic prominently bent, with broad posterior expansion, and large anterior cartilaginous knob*. Primitively it has a slight bend, a slightly expanded posterior end, and a small anterior cartilage.

(12) *Adductor hyomandibulae* (AH) present (shared with Esocidae, *Dallia*, some osmerids [*Spirinchus* and *Thaleichthys*], and most Alepocephaloidea). Primitively there is no AH (see also Winterbottom, 1974).

***Lepidogalaxias* + Galaxiidae + Aplochitonidae**

(8B) *Lateral foramen for hyomandibular branch of facial nerve at ventral end of lateral strut of hyomandibular* (see synapomorphy 8 for details). A lateral strut is absent in *Lovettia*.

(13) *Mesopterygoidal teeth reduced in number or absent* (Fig. 13: 13A). These teeth are also absent in esocoids, salmonids, salangids, alepocephalids, and the Argentinoidea, and are few in platytroctids. Primitively in galaxioids (Retropinnidae + Prototroctidae) and osmerids the entire medioventral surface of the mesopterygoid bears numerous teeth (Williams, 1987).

(14) *Metapterygoid small with axe-shaped endochondral part* (shared with *Novumbra, Dallia*, and some Argentinoidea). It is smaller in the latter three taxa, and in *Novumbra* and *Dallia* overlaps a unique anteroventral wing of the hyomandibular. Primitively, the metapterygoid is somewhat large with a prominent rectangular or lunate endochondral section. Johnson & Patterson (1996) believe that a greatly reduced metapterygoid that fails to contact the symplectic and hyomandibular unites only *Lovettia* and *Lepidogalaxias*. However, the metapterygoid is also relatively small in *Aplochiton* and the Galaxiidae. Although the metapterygoid does not contact the hyomandibular and symplectic in *Lovettia* and *Lepidogalaxias*, this is also true of the equally small

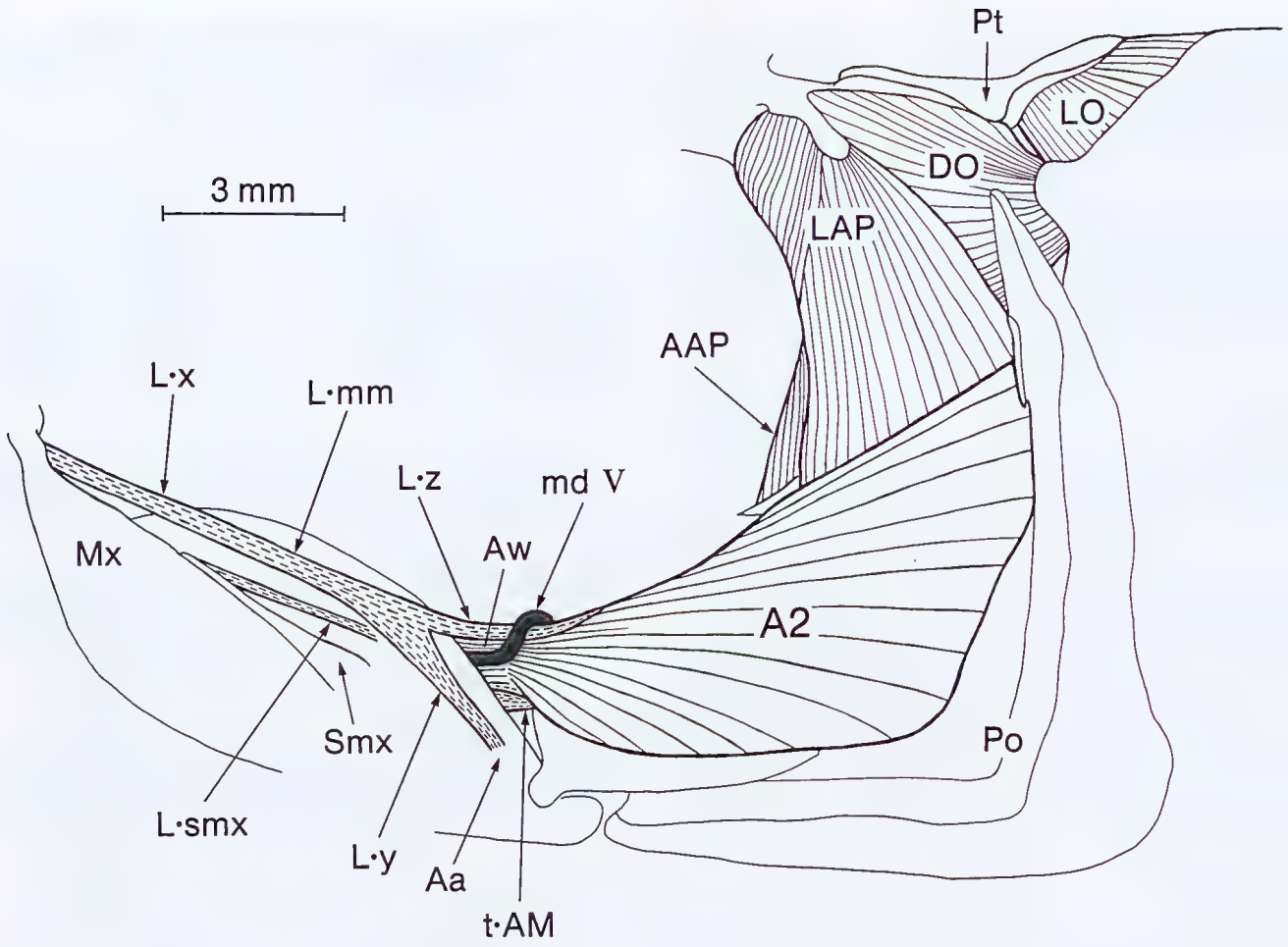

Fig. 14. Lateral view of external muscles of left suspensorium in *Hypomesus pretiosus* (UAMZ 3515, 135.4 mm) to illustrate elements commonly referred to in text.

galaxiids *Galaxias paucispondylus* (Williams, 1987), *Galaxiella pusilla* and *G. nigrostriata* (Frankenberg, 1969). Furthermore, the metapterygoid does not contact the symplectic and just barely contacts the hyomandibular in *Aplochiton taeniatus* (Fig. 6), and contacts neither the symplectic nor the hyomandibular in *A. zebra* (McDowall, 1969, fig. 3).

(15) *Adductor mandibulae with unique maxillo-mandibular ligament.* Osmerids (Fig. 14) and more generalised and primitive clupeomorphs and elopomorphs have the primitive state. The ostariophysan pattern is an autapomorphy (Fink & Fink, 1981; Howes, 1985). Primitively, there is one external division of the adductor mandibulae, section A2. There is also an Aw section (= intramandibularis) anterior to A2 that inserts in and fills the Meckelian fossa on the medial surface of the lower jaw. Section A2 inserts mainly on the medial surface of the lower jaw (via a tendinous aponeurosis) and connects with the maxilla and the posterolateral surface of the lower jaw via the maxillo-mandibular ligament (= ligamentum primordium, labelled L.x, L.y, and L.z on Fig. 14). In *Lepidogalaxias*, Galaxiidae and Aplochitonidae the maxillo-mandibular ligament extends from the anterolateral end of section A2 to the maxilla. However, the part of the maxillo-mandibular ligament attaching onto the lower jaw is unlike the outgroups. The section extending to the angulo-articular (Figs 9–12: L.y) is reduced so there is almost no separate segment (Fig. 14: L.z) extending from the adductor mandibulae to the main part (L.x–L.y) of the maxillo-mandibular ligament. The maxillo-mandibular ligament also has a new section (Figs 9–12: L.w) extending anteroventrally from the intersection of L.x and L.y to the coronoid process (dentary).

(16) *Tendinous aponeurosis on which medial fibres of section A2 of adductor mandibulae insert not connected with posteriormost end of maxillo-mandibular ligament or barely connected with it* (shared with the argentinoid *Bathylagus*). The state in *Lovettia* could not be determined mainly because of small specimen size. Primitively, there is a distinct connection between the anterodorsal edge of the tendinous aponeurosis (before it bifurcates anteriorly) and the posteriormost end of the maxillo-mandibular ligament.

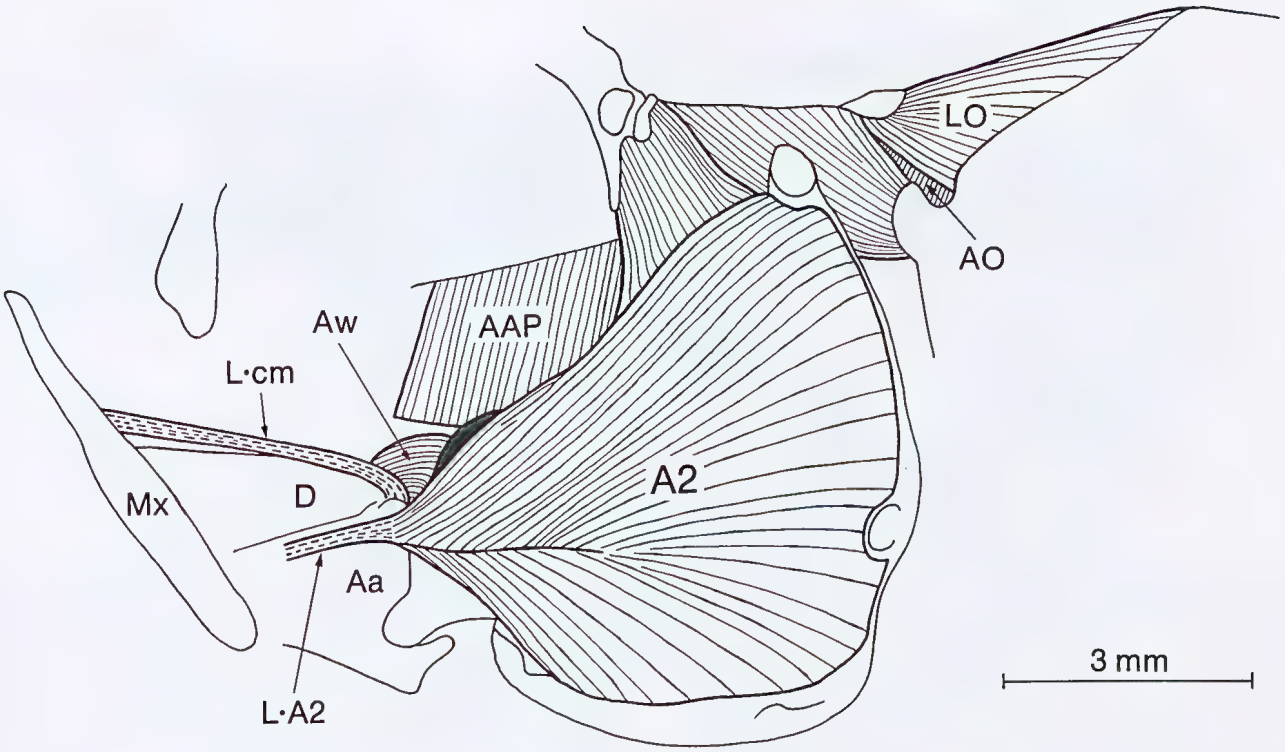

Fig. 15. Lateral view of external muscles of left suspensorium in *Umbra limi* (UAMZ 3752, 67.4 mm).

(17) *Short ligament between posteromedial surface of maxilla and coronoid process of lower jaw* (Fig. 9: L). Although the posteromedial surface of the maxilla is connected to the coronoid process via connective tissue in the other salmoniforms, none has a similar ligament. All esocoids have a ligament between the coronoid process and maxilla (Figs 15, 16, 18, 19: L.cm), but it is not the maxillo-mandibular ligament since both occur in *Esox* (Fig. 18). It is not homologous with the galaxioid ligament because it is much longer and flatter, extends anteroposteriorly, and inserts farther anteriorly on the maxilla. Also, connective tissue extends between the posteromedial surface of the maxilla and the coronoid process, but there is no ligament. This coronoid-maxilla ligament is a new esocoid synapomorphy (Williams, 1987).

(18) *Adductor arcus palatini expanded anteriorly so insertion includes dorsal surface of mesopterygoid* (shared with Esocoidei, Salmoninae, and Argentinoidea). Primitively, it is posterior and inserts on the hyomandibular, and usually the metapterygoid (see also Winterbottom, 1974).

Galaxiidae + Aplochitonidae

(7B) *Ectopterygoid greatly reduced or absent and largely or completely replaced by prominent ligament* (see also synapomorphy 7 for details). The replacement may not be complete in all specimens, in that a small, splint-like ectopterygoid can be present in *Lovettia* according to McDowall (1969) and G. David Johnson (personal communication); however, the character would still apply since the new ligament is found in *Lovettia*.

(9B) *Lateral strut of hyomandibular robust, forming a lateral shelf* (see synapomorphy 9 for details). A lateral strut is absent in *Lovettia*.

(13B) *Mesopterygoid with large ventroanterolaterally curving teeth in single anteromedial row opposing large posterodorsally curving teeth around the edge of the basihyal* (Fig. 17). Primitively in galaxioids (Retropinnidae + Prototroctidae) and osmerids the teeth are distributed over the entire medioventral surface of the mesopterygoid, they are ventrolaterally directed (see also Williams, 1987), and they oppose dorsomedially-directed teeth on the basihyal and basibranchials. Among other salmoniforms, some platytroctids have mesopterygoidal teeth, but they are smaller than in

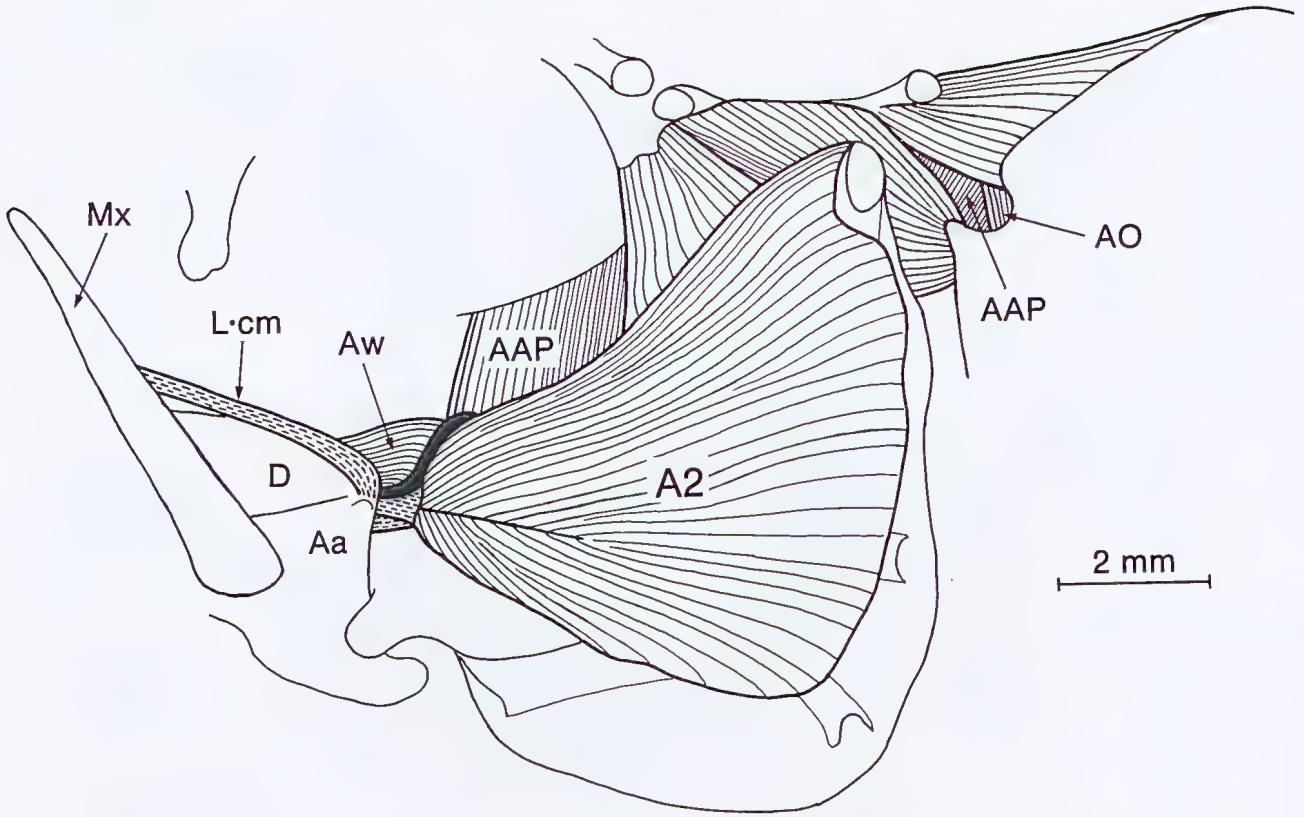

Fig. 16. Lateral view of external muscles of left suspensorium in *Umbra krameri* (UAMZ 3727, 63.3 mm).

galaxiids and aplochitonids and oppose small teeth on the basibranchials. Salmonines have enlarged basihyal teeth, but they are smaller than in galaxiids and aplochitonids and oppose large vomerine teeth (mesopterygoids and basibranchials are edentulous).

(19) *Palatine lacks teeth and the dermopalatine is absent or greatly reduced* (shared with adult *Plecoglossus* and some alepocephaloids; see also Markle, 1976 and Matsui & Rosenblatt, 1987). Primitively the palatine consists of a tubular, endochondral autopalatine, and a flattened, tooth-bearing dermopalatine.

(20) *Section A2 of adductor mandibulae has dorsomedial subdivision* (shared with *Plecoglossus* and possibly *Dallia*). Homology is suggested by a similar origin and insertion, and because the mandibular branch of the trigeminal nerve lies medial to the subdivision. The state in *Lovettia* could not be determined mainly because of small specimen size. Primitively in salmoniforms and lower teleosts A2 is not subdivided. The dorsomedial subdivision in *Plecoglossus* is not homologous with that in galaxioids because its fibres converge anteriorly on a separate tendon that extends anteriorly to join the tendon on which the dorsolateral fibres of the main muscle mass converge (Williams, 1987). *Dallia* has what might be interpreted as either a dorsomedial subdivision of section A2 (Fig. 19: A2.dm?) or a posteromedial expansion of section Aw (Williams, 1987). Either way it is unlikely to be homologous with the muscle in galaxiids and aplochitonids because it originates mainly from the hyomandibular (versus metapterygoid) in a unique way, inserts on a separate tendon that inserts on the medial surface of the lower jaw, and because the mandibular branch of the trigeminal nerve is lateral to it (versus medial).

(21) *Section A2 of adductor mandibulae originates partly from posterior surface of lateral strut of hyomandibular* (shared with the alepocephalid *Leptoderma*). Although a lateral strut is absent in *Lovettia* the origin of Section A2 of the adductor mandibulae is the same as in *Aplochiton* and the Galaxiidae. Primitively it originates from the anterior face of the strut.

Critique of competing hypotheses of galaxioid relationships

Although substantial evidence supports the hypothesis that the Retropinnidae + Prototroctidae form a monophyletic group (McDowall, 1969; Patterson, 1970; Nelson, 1972; Rosen, 1974; Berra *et al.*, 1982; Fink, 1984; Nelson, 1984; Begle, 1991) and that the Galaxiidae + Aplochitonidae form a monophyletic group (McDowall,

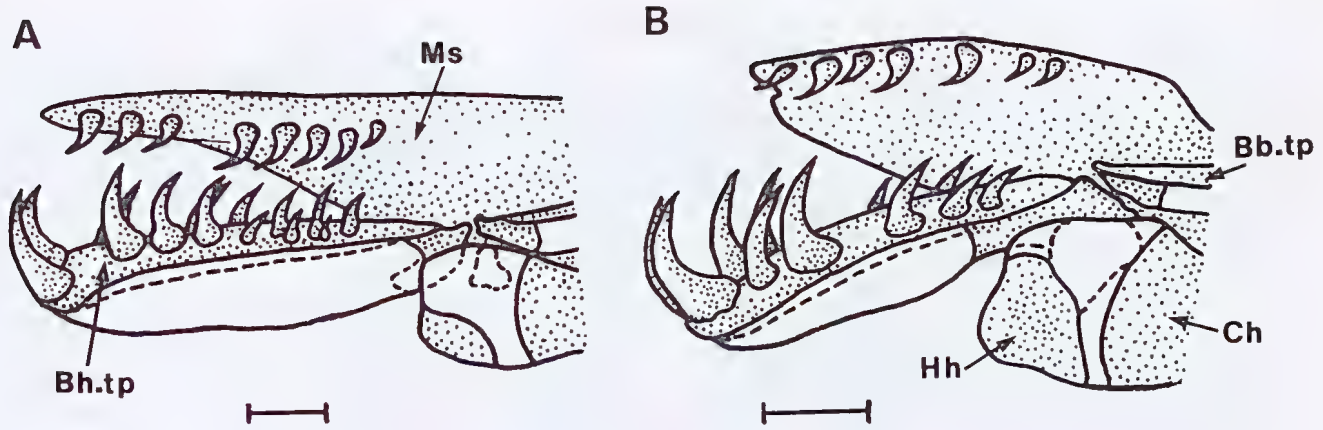

Fig. 17. Medial view of right mesopterygoid and basihyal, *in situ*, in (A) *Aplochiton taeniatus* (NMC 76-0393, 110.5 mm) and (B) *Galaxias brevipinnis* (UAMZ 4608, 93.0 mm) to show bite. Scale = 1.0 millimetre.

1969; Patterson, 1970; Nelson, 1972; Rosen, 1974; Fink, 1984; Begle, 1991), the relationship of each assemblage to other salmoniforms is debatable. As noted earlier, most workers place Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae in a monophyletic group. Rosen (1974) believed otherwise. He united the Retropinnidae, Prototroctidae, Osmeridae, and Salangidae partly because he claimed that they share a unique "stegural" formed by fusion of the rudimentary neural arch(es) of PU1 with the first uroneural. Fink & Weitzman (1982) analysed Rosen's (1974) evidence and noted exceptions: some of the above taxa have rudimentary neural arches fused with PU1 (in addition to fusion with the uroneural), and some galaxiids and aplochitonids have fusion of the rudimentary neural arches with the first uroneural (and PU1).

Rosen (1974) also used hyobranchial evidence to unite retropinnids, prototroctids, and osmeroids. It is hard to tell from his text what synapomorphies he is using (see also Fink & Weitzman, 1982). One is apparently (p. 313) "a blunt, somewhat elevated median ridge [on the basibranchial toothplate] except when [the] tooth plate is greatly expanded." I found that although the toothplate arches dorsally there is no "blunt ... median ridge." An arched, similarly shaped basibranchial toothplate is also present in many primitive teleosts (e.g., *Elops* and *Osteoglossum*). Another synapomorphy is (p. 313): "Basihyal fangs in forms with unreduced dentition [are] large, arranged in alternating positions on [the] right and left side, and tending to form a single large terminal tooth." I do not find this convincing. First, two osmeroids (*Mallotus* and *Plecoglossus*) have reduced basihyal

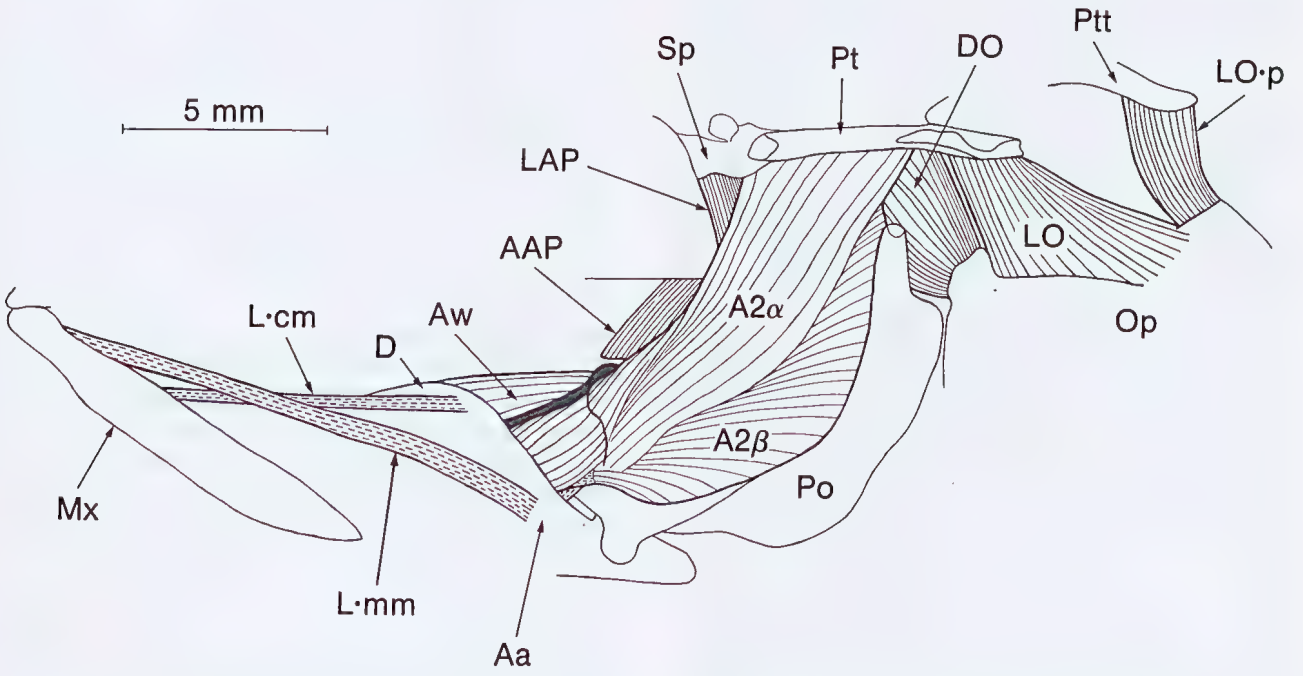

Fig. 18. Lateral view of external muscles of left suspensorium in *Esox lucius* (UAMZ 4878, 103.0 mm).

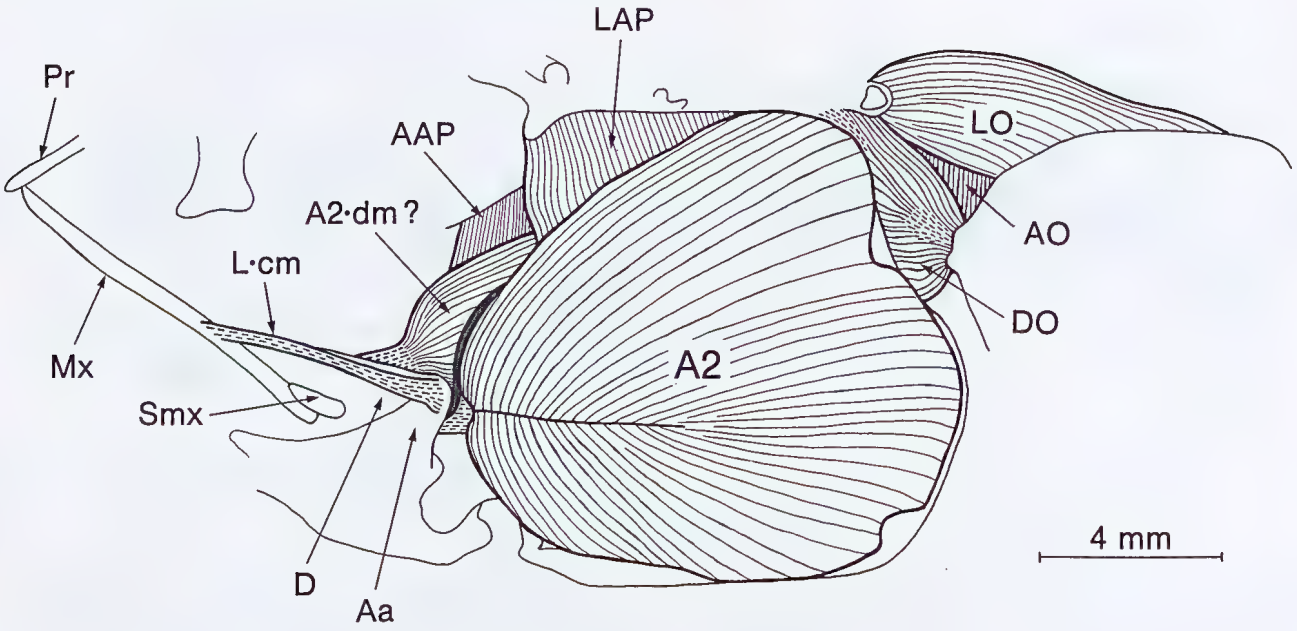

Fig. 19. Lateral (slightly dorsal) view of external muscles of left suspensorium in *Dallia pectoralis* (UAMZ 3737, 115.8 mm).

dentition and small teeth, and second, the teeth on the right and left sides of the basihyal do not alternate in all osmeroids (*sensu* Rosen, 1974), nor do they usually all alternate even when alternation is present. For example, in my specimens of *Thaleichthys* the teeth are arranged in right and left pairs (except the anteriormost pair), and except for the anteriormost pair resemble the pattern in the salmonines, galaxiids, and aplochitonids. Also, when the teeth alternate it is usually the anterior teeth; the posterior teeth are paired. The alternating anterior teeth may be the result of the anterior end of the basihyal being narrow, crowding the anterior teeth (not clearly illustrated by Rosen but visible in my specimens). A terminal tooth is absent in my specimens of *Hypomesus* and *Prototroctes*; instead, there is a terminal pair as in the salmonines, galaxiids, and aplochitonids. Some salmonines (*Salvelinus fontinalis, S. namaycush*) also have a terminal tooth. Another apparent Rosen synapomorphy is that in osmeroids the fifth epibranchial is fused ventrally to the posteroventral end of the fourth. Primitively, the fifth epibranchial is next to, but not fused with the posteroventral end of the fourth (Nelson, 1967a). However, there is no fusion of epibranchial five with epibranchial four (although they are adjacent) in several osmeroids illustrated by Rosen, including *Stokellia* and *Plecoglossus*. Epibranchial five is distinctly separate from epibranchial four in my specimens of *Prototroctes*, a taxon not illustrated by Rosen. Also, in my specimens of *Retropinna retropinna* the ventral end of epibranchial five closely abuts the posteroventral end of epibranchial four but there is a line between the two, suggesting no fusion (see Rosen's fig. 16F, in which he shows fusion in *R. retropinna*).

Rosen (1974) united the Galaxiidae (my Galaxiidae + Aplochitonidae) with the Salmonidae and placed them in their own superfamily, Salmonoidea. According to him they share enlarged, fang-like teeth around the margin of the basihyal (arranged in right and left pairs and terminating anteriorly as a single pair) and a basibranchial that is edentulous or has just a few teeth. This basihyal character is suspect for several reasons. First, other salmoniforms have enlarged marginal basihyal teeth, including the Retropinnidae, Prototroctidae, Osmeridae, and Argentinidae. As mentioned earlier, some members of the latter families also have basihyal teeth arranged in right and left pairs ending anteriorly in a terminal pair. Fink & Weitzman (1982) also noted that about half the galaxiids they examined had alternating tooth pairs along the margin of the basihyal and a single terminal tooth, a state similar to the condition Rosen claimed was an osmeroid (*sensu* Rosen, 1974) synapomorphy. Although the Salmoninae have paired basihyal teeth, some (*Salvelinus fontinalis, S. namaycush*) have a terminal tooth as in many osmeroids. Basibranchial teeth are also absent or few in salangids, *Lepidogalaxias*, the Argentinoidei, and stomiiforms. Rosen (1974) also noted that, unlike the condition in salmonines, the basibranchial toothplate in galaxiids and aplochitonids is not fused with the second endoskeletal basibranchial. Within the Salmonidae, only the Salmoninae exclusive of the Eocene fossil *Eosalmo* (Wilson & Williams, 1992) have enlarged basihyal teeth; the Thymallinae and Coregoninae have numerous small teeth scattered randomly over both the basihyal and basibranchials. Furthermore, numerous salmonines have basibranchial teeth (see Stearley & Smith, 1993), including

Oncorhynchus clarki, which has up to 52 according to Behnke (1992).

Rosen also cited epibranchial evidence. He claimed that fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial was a galaxiid + salmonid synapomorphy. All galaxiids and aplochitonids illustrated by Rosen (and those examined by me) had this state. However, Rosen found such fusion only in one salmonid, *Prosopium cylindraceum*. All the other species possessed the primitive state in which the fifth epibranchial is separate from the fourth. None of the salmonids that I examined possessed fusion, including *P. williamsoni*. Another synapomorphy was the lack of an uncinate process on the fourth epibranchial. But not all galaxiids lack an uncinate process. It is present in *G. anomalus* (= *G. vulgaris*), *G. delfini* (= *G. platei*) (Fink & Weitzman, 1982), and in *G. paucispondylus* (personal observation). Besides salmonids, an uncinate process is absent in some umbrids (*Umbra*), some osmerids (*Hypomesus, Mallotus*, and possibly *Allosmerus*), salangids, prototroctids, some retropinnids (*Retropinna retropinna*), *Lepidogalaxias*, and many Argentinoidei (personal observation; see also Rosen, 1974; Greenwood & Rosen, 1971; Begle, 1992). Another synapomorphy was the absence of a levator process on the fourth epibranchial. According to Rosen, the process is the insertion area for the fourth external levator muscle. This character is difficult to interpret. Fink & Weitzman (1982) questioned Rosen's definition of a levator process noting (p. 82) that "In many primitive euteleosts [the dorsolateral surface of the fourth epibranchial] is separated from the ventrolateral extremity of the bone by a concavity, so that the area of [the insertion of the levator muscle] may be termed a process. Rosen's character, "absence of a levator process", might better be defined as loss of this concavity; the area of levator attachment remains unchanged, although in descriptive terms it is no longer a process." I concur with Fink & Weitzman's interpretation. As defined by Fink & Weitzman the "Absence of this concavity" is shared with salmonids, galaxiids (*sensu* Rosen, 1974), the retropinnids *R. retropinna* and *Stokellia*, prototroctids, *Salangichthys* (Salangidae), and all esocoids except *Umbra* (personal observation; Fink & Weitzman, 1982).

The neotenic salangids are sometimes placed with galaxioids. Greenwood *et al.* (1966) included them within the Galaxioidei, but why they did this is unclear from their text. Weitzman (1967) suggested placing salangids in a group separate from osmerids, galaxioids, and stomiatoids. Nelson (1970) noted similarities with the Argentinoidea. McDowall (1969) concluded that salangids are not galaxioids. Rosen (1974) placed them *incertae sedis* within his Osmeroidea. Howes & Sanford (1987) considered salangids to be the sister group of their Osmeridae. Roberts (1984) placed them in the superfamily Salangoidea within the order Salmoniformes (coordinate with Osmeroidea and Salmonoidea). Fink (1984) said that salangids were galaxioids if one accepted their shared reductive traits, or osmeroids if one accepted their shared (p. 204) complex caudal skeleton character. Begle (1991) placed salangids with galaxioids after conducting a phylogenetic analysis using PAUP. Suspensorial evidence is equivocal, and I placed them *incertae sedis* within the galaxioid + osmeroid + argentinoid clade (Williams, 1987). However, Johnson & Patterson (1995, 1996, also G. David Johnson, personal communication) recently redefined many of Begle's (1991) characters and present new and convincing evidence that salangids belong in the Osmeridae, and are the sister group of *Mallotus*.

Another controversy is whether or not *Lepidogalaxias* is a galaxioid. Nelson (1972) noted that the cephalic pitlines in *Lepidogalaxias* resemble those of the esocoid *Dallia*. I agree, but *Dallia* has a more extensive pattern of cephalic canals than does *Lepidogalaxias*. Preopercular, infraorbital, supraorbital, and temporal canals are present in *Dallia*, but only a preopercular canal is found in *Lepidogalaxias*. The pattern of the pitlines is also different upon closer examination (e.g., compare Nelson's figures of *Dallia* with fig. 16 in Frankenberg, 1969).

Rosen (1974) placed *Lepidogalaxias* in the Esocoidei. I question this hypothesis, as did Fink & Weitzman (1982) who state (p. 80) that "Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae [= Esocoidei], only four appear to be appropriate for inference of relationship between those groups: lack of a mesocoracoid, lack of pyloric caeca, a single rudimentary neural arch and spine over PU1, and a single uroneural." Since I am unsure why they singled out these characters the following is a list of Rosen's synapomorphies (1974: 311): (1) "Dorsal fin posterior in position, over anal fin" (shared with Galaxiidae, Retropinnidae, Salangidae and many Argentinoidei). (2) "no adipose dorsal fin" (shared with Galaxiidae, some Salangidae, and many Argentinoidei). (3) "maxillary edentulous" (shared with galaxiids, aplochitonids, prototroctids, most retropinnids, and many other salmoniforms; see McDowall, 1976, 1979; Nelson, 1994). (4) "with or without a supramaxilla" (Rosen listed both states and the derived state is ambiguous). (5) "endopterygoid [= mesopterygoid] edentulous" (shared with Salmonidae, Salangidae, Alepocephalidae, Argentinoidea, and some members of the galaxiid genus *Neochanna*). (6) "no mesocoracoid" (shared with Galaxiidae, Aplochitonidae, Retropinnidae, Prototroctidae, Salangidae, and many Argentinoidei; see Markle, 1976; Nelson, 1994; Roberts, 1984). (7) "no pyloric caeca" (shared with salangids, retropinnids, prototroctids, some galaxiids, and some aplochitonids; see McDowall, 1971; McDowall & Frankenberg, 1981). (8) "a single large, oval, strongly dentigerous tooth plate supported by the fourth infrapharyngobranchial and fourth epibranchial" (shared with Salmonidae, Stomiiformes, and many higher teleosts; see Rosen, 1973, 1974; Weitzman, 1974). A similar, but smaller, narrower toothplate with smaller teeth is found in many salmoniforms, including salangids, most osmerids (including *Plecoglossus*), retropinnids, and prototroctids. In galaxiids and aplochitonids there are usually several smaller tooth-plates in the area usually occupied by a

single large tooth-plate (see also Rosen, 1974). (9) "fourth epibranchial always somewhat reduced and without a distinct posterodorsal process for the external branchial levator muscle." I discussed this character above. The term "somewhat reduced" is unclear if one examines Rosen's figures of this structure. Although there is no distinct posterodorsal process in *Lepidogalaxias* and esocoids (excluding *Umbra*) this can be said of other salmoniforms he illustrates (some salmonids and retropinnids). The fourth epibranchial in *Lepidogalaxias* is also only broadly similar to that in the esocoids and more closely resembles the one in galaxioids. (10) "never more than a single rudimentary neural arch and spine over PU1." One rudimentary neural arch is found in some osmerids (Rosen, 1974, fig. 28B), many salmonids (Rosen's figures 25A, B, and C), some galaxiids and aplochitonids (Rosen's figures 18 and 19), some Argentinoidea (Greenwood & Rosen, 1971; Markle, 1976), and possibly some salangids (Rosen, 1974, fig. 26B). Rudimentary neural arches in galaxiids and aplochitonids are different from those in *Lepidogalaxias* and esocoids because they are larger and usually fused ventrally with a compound centrum (but in Rosen's fig. 19B of *Lovettia* the two rudimentary neural arches are autogenous). A rudimentary neural arch is also apparently fused ventrally to the underlying centrum in some specimens of *Lepidogalaxias* (Rosen, 1974, fig. 24C), which in this respect resembles galaxioids. (11) "a single, long, straplike uroneural." Some galaxiids and aplochitonids have one uroneural similar in shape to that in some umbrids (Rosen's figures 18D, 19C, 21, and 23). Rosen (p. 293) also noted that some specimens of *Lepidogalaxias* had "anterodorsal acuminate processes" on the uroneural that resemble those in esocoids. However, other salmoniforms, including galaxioids, have similarly shaped processes (figures in Rosen, 1974).

Fink (1984) hypothesised that *Lepidogalaxias* may be the sister group of the Neoteleostei because they share a retractor dorsalis muscle and an occipital condyle composed of both basioccipital and exoccipital. Both are neoteleostean synapomorphies according to Fink & Weitzman (1982). Fink (1984) said that *Lepidogalaxias* was not a neoteleost because it lacked both a rostral cartilage or its homologue and teeth with a unique attachment mode. He also claimed that salmonids are a possible sister group of neoteleosts since they share a similar occipital condyle and salmonids have a homologue of the rostral cartilage. Salmonids are not neoteleosts, according to Fink, because they lack teeth with a unique attachment mode and a retractor dorsalis. Because of this uncertainty Fink placed Salmonidae, *Lepidogalaxias*, and Neotelostei in an unresolved trichotomy.

The retractor dorsalis is a bilaterally paired muscle extending from the anterior vertebrae to the dorsal gill arch elements. It represents a specialisation of the feeding mechanism that allows more independent movement of the dorsal gill-arch elements and their toothplates (Nelson, 1967a,b; Rosen, 1973), and occurs in the osteoglossomorph *Pantodon*, some muraenid eels (Elopomorpha), some ostariophysans (siluriforms and some cyprinids), neoteleosts, and in non-teleosts such as *Amia* and *Lepisosteus* (Nelson, 1967a; Rosen, 1973, 1985; Winterbottom, 1974; Johnson, 1992). Its presence in *Lepidogalaxias* may be related to an ability to bend the neck at a sharp angle during feeding. Facilitating this skill are wide spaces between the exoccipital, first vertebra, and second vertebra, and slightly narrower spaces between the other cervical vertebrae. Also possibly related to this ability is an occipital condyle composed of both basioccipital and exoccipital. This feature is shared with the osteoglossomorph *Hiodon*, salmonines, and neoteleosts (see also Rosen, 1985; Johnson, 1992). In these taxa a distinct tripartite occipital joint exists involving both exoccipital and basioccipital. The contact of the exoccipital with the centrum of the first vertebra is via a cartilage-covered condyle or surface on each exoccipital that contacts a separate facet (usually) on the dorsolateral corners of the anterior end of the centrum. The rest of the anterior end of the centrum contacts the basioccipital. The occipital joint in *Lepidogalaxias*, however, is different, and probably not homologous. The basioccipital forms almost the entire joint surface, with two wing-like extensions of each exoccipital overlapping each dorsolateral corner of the anterior end of the first centrum. The contact area of the exoccipital with the vertebra is smaller than in most teleosts with such a joint and is more lateral. The exoccipital also lacks a distinct cartilage-covered condyle or facet where it contacts the first vertebra, which also lacks a facet at the contact point. The exoccipital "wings" resemble the posterolateral extensions of the exoccipitals that approach the first vertebra in some galaxiids (e.g., *Galaxias brevipinnis*).

Also supporting my hypothesis that the retractor dorsalis of *Lepidogalaxias* is not homologous with the retractor dorsalis of neoteleosts is Johnson's (1992) new synapomorphy uniting the Neoteleostei: insertion of the third internal levator muscle on the fifth upper pharyngeal toothplate. In all non-neoteleosts with a "retractor dorsalis" that Johnson examined, including *Lepidogalaxias*, the third internal levator inserts on the fourth pharyngobranchial cartilage. Johnson interprets the shift in insertion of the third internal levator in neoteleosts as related to the advent of the neoteleostean retractor dorsalis. He hypothesises that this new arrangement (p. 11) "provides for a forward pull on the fifth [upper pharyngeal] toothplate acting antagonistically to the backward pull of the retractor dorsalis on that element." He concludes that (p. 12) the "Lack of the associated neoteleost modification is at least consistent with an independent origin of the 'retractor dorsalis' of *Lepidogalaxias*, although it does not specifically refute the *Lepidogalaxias*—neoteleost hypothesis."

As a final point I will briefly discuss paedomorphosis in galaxioids. Reductive evolution is common in teleosts, and galaxioids are no exception. If you define a reductive character as one that involves obvious truncation of development (Begle, 1991), only four (19%) of my 21

characters are clearly reductive (2, 4, 13, and 19). Paedomorphosis in the galaxioids, at least regarding the suspensorium and its muscles, is not as common as one might predict after reading earlier studies. For example, 20 (54%) of the 37 characters that supported Begle's (1991) hypothesis of galaxioid relationships were reductive. His characters were osteological with two exceptions (24, 51). Other galaxioid studies also relied on osteological characters (e.g., McDowall, 1969), hence the conclusion that galaxioids exhibit extensive paedomorphosis. This is true if one considers only osteology. However, an important finding of my study is that galaxioids exhibit little paedomorphosis regarding the muscles of the suspensorium. This is also true of osmerids and salangids (see also Williams, 1987). The only galaxioid reductive muscle character is loss of the supramaxillary ligament, a feature correlated with loss of the supramaxillae. These findings illustrate the value of examining new anatomical systems when studying problematic taxa. Paedomorphosis in one organ system is not necessarily correlated with paedomorphosis in another, and not all functional units of the skeleton appear to exhibit this phenomenon to the same degree. This is not surprising since characters within the same species evolve at different rates.

Conclusions

This study provides significant new osteological and myological information, some of which constitutes important new evidence bearing on galaxioid intrarelationships and the phylogenetic position of *Lepidogalaxias*. My phylogeny, based strictly on the bones and muscles of the suspensorium, suggests that the galaxioids are monophyletic and include *Lepidogalaxias*. *Lepidogalaxias* is the sister group of Galaxiidae + Aplochitonidae based particularly on synapomorphies of the adductor mandibulae. The following galaxioid pattern, based on the suspensorium and its muscles, is proposed: ([Retropinnidae + Prototroctidae] + [*Lepidogalaxias* + (Galaxiidae + Aplochitonidae)]).

Placement of the southern salmoniforms in one group has significance for historical biogeography since the number of events, dispersal or vicariance, which must be assumed to account for their distribution is fewer if *Lepidogalaxias* is a galaxioid rather than an esocoid. Their distribution across the southernmost end of the Southern Hemisphere could be explained either by very ancient vicariant events (Rosen, 1974) or by some form of transoceanic dispersal (McDowall, 1984; Berra *et al.*, 1995). In support of the latter hypothesis is the observation that marine stages are found in numerous galaxioids (McDowall, 1984), including the disjunct species *Galaxias maculatus* from eastern and western Australia, New Zealand, South America and associated oceanic islands. Berra *et al.* (1995) provide convincing new genetic evidence that distribution of *G. maculatus* is best interpreted as due to dispersal through the sea.

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Appendix 1. Input data matrix of taxa, characters, and character states analysed using PAUP version 3.1.1. (Swofford, 1993). Character numbers correspond to those in the text.

	Characters																			
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Retropinnidae	1	1	1	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	0	0	0
Prototroctidae	1	1	1	1	1	1	1	2	1	1	1	1	0	0	0	0	0	0	0	0	0
Lepidogalaxias	1	1	1	1	1	1	2	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Galaxiidae	1	1	1	1	1	1	3	1	2	0	0	0	2	1	1	1	1	1	1	1	1
Aplochitonidae	1	1	1	1	1	1	3	1	2	0	0	0	2	1	1	1	1	1	1	1	1

Appendix 2. The following is a list of specimens examined and their method of preparation: cs = cleared and stained for cartilage and bone, csb = cleared and stained for bone only, ds = dry skeleton, r = radiographed, md = muscle dissection, • = extinct taxon, f = fossil. Number of galaxioid specimens examined are indicated. For detailed information, including catalogue numbers, refer to Williams, 1987. Supraspecific taxa are listed roughly phylogenetically while species are listed alphabetically

SALMONIFORMES

Esocidae
- *Esox lucius* (cs, ds, md)
- *E. masquinongy* (cs, md)
- • *E. tiemani* (f)

Umbridae
- *Dallia pectoralis* (cs, md)
- *Novumbra hubbsi* (cs, md)
- • *N. oregonensis* (f)
- *Umbra krameri* (cs, md)
- *U. limi* (cs, md)
- *U. pygmaea* (csb, md)

Salmonidae
- *Brachymystax coregonoides* (r)
- *B. lenok* (md)
- *Coregonus artedii* (cs, md)
- *C. clupeaformis* (cs, md)
- • *Eosalmo driftwoodensis* (f)
- *Oncorhynchus gairdneri* (cs)
- *O. kisutch* (cs)
- *O. nerka* (cs, md)
- *Prosopium cylindraceum* (md)
- *P. williamsoni* (cs, md)
- *Salmo trutta* (cs, ds, md)
- *Salvelinus alpinus* (ds)
- *S. fontinalis* (cs, md)
- *S. namaycush* (cs)
- *Stenodus leucichthys* (cs, ds, md)
- *Thymallus arcticus* (cs, md)

Osmeridae
- *Allosmerus elongatus* (cs, md)
- *Hypomesus olidus* (cs)
- *H. pretiosus* (cs, md)
- *Mallotus villosus* (cs, f, md)
- *Osmerus mordax* (cs, md)
- *Plecoglossus altivelis* (cs, md)
- *Spirinchus starksi* (cs, md)
- *S. thaleichthys* (cs, md)
- *Thaleichthys pacificus* (cs, md)

Salangidae
- *Salangichthys ishikawae* (cs, md)
- *S. microdon* (cs, md)
- *Salanx cuvieri* (md)
- *S. prognathus* (cs, md)

Retropinnidae
- *Retropinna retropinna* (2 cs, 3 md)

Prototroctidae
- *Prototroctes maraena* (2 cs, 2 md)

Lepidogalaxiidae
- *Lepidogalaxias salamandroides* (1 cs, 2 r, 2 md)

Galaxiidae
- *Brachygalaxias bullocki* (1 cs, 1 md)
- *Galaxias brevipinnis* (1 cs, 1 md)
- *G. fasciatus* (2 md)
- *G. maculatus* (2 cs, 3 md)
- *G. paucispondylus* (1 cs, 1 md)
- *Neochanna apoda* (1 cs, 1 md)

Aplochitonidae
- *Aplochiton taeniatus* (1 cs, 1 md)
- *Lovettia sealii* (2 cs, 6 md)

Argentinidae
- *Argentina silus* (cs, md)

Bathylagidae
- *Bathylagus pacificus* (cs, md)

Opisthoproctidae
- *Dolichopteryx longipes* (cs, md)
- *Macropinna microstoma* (cs, md)
- *Opisthoproctus soleatus* (csb, md)

Platytroctidae
- *Holtbyrnia latifrons* (cs, md)
- *Mirorictus taningi* (cs, r, md)
- *Pellisolus facilis* (cs, md)
- *Platytroctes apus* (cs, r, md)
- *Sagamichthys abei* (cs, md)
- *Searsia koefoedi* (cs, r, md)
- *Searsioides multispinus* (cs, md)

Alepocephalidae
- *Alepocephalus bairdii* (cs)
- *A. tenebrosus* (cs, md)

Appendix 2. Continued.

Bajacalifornia burragei ..... (cs, md)
Bathylaco nigricans ..... (cs, r, md)
Bathylaco sp. ..... (r, md)
Bathytroctes microlepis ..... (cs, md)
Binghamichthys (= Talismania) aphos ..... (cs, md)
Conocara mcdonaldi ..... (cs, md)
Leptoderma macrops ..... (cs, md)
Narcetes stomias ..... (cs, md)
Photostylus pycnopterus ..... (cs, md)
Rouleina maderensis ..... (cs, md)
R. nudus ..... (md)
Talismania antillarum ..... (cs, md)
T. bifurcata ..... (md)
Xenodermichthys copei ..... (cs, r, md)

OTHER TELEOSTEI

Pholidophoriformes •
• *Pholidophorus* sp. ..... (f)
Osteoglossiformes
• *Eohiodon rosei* ..... (f)
Hiodon alosoides ..... (cs, md)
Osteoglossum bicirrhosum ..... (cs, md)
Pantodon buchholzi ..... (md)
• *Phareodus testis* ..... (f)
Xenomystus nigri ..... (cs, md)
Elopiformes
Elops affinis ..... (md)
E. hawaiensis ..... (cs)
Megalops cyprinoides ..... (cs, md)
Ellimmichthyiformes •
• *Diplomystus* ..... (f)
Clupeiformes
Chirocentrus dorab ..... (csb, md)
Alosa pseudoharengus ..... (cs)
A. sapidissima ..... (csb, md)
Anodontostoma chacunda ..... (md)
Clupea harengus ..... (cs, md)
Dorosoma petenense ..... (cs)
Dussumieria hasselti ..... (csb, md)
Etrumeus teres ..... (csb)
Harengula thrissina ..... (csb)
Hyperlophus sprattellides ..... (csb)
Ilisha furthii ..... (csb, md)
Jenkinsia stolifera ..... (csb)
• *Knightia eocaena* ..... (f)
• *Knightia* sp. ..... (f)
Nematalosa erebi ..... (csb)
Odontognathus compressus ..... (csb)
O. panamensis ..... (csb)
Amentum devisi ..... (md)
Anchoa mundeoloides ..... (md)
A. panamensis ..... (csb)
Cetengraulis mysticetus ..... (csb)
Engraulis sp. ..... (csb)
Thryssa (= Thrissocles) hamiltoni ..... (csb, md)
Gonorhynchiformes
Chanos chanos ..... (cs, md)
• *Notogoneus osculus* ..... (f)
Cypriniformes
Catostomus commersoni ..... (md)
Couesius plumbeus ..... (cs)
Notropis blennius ..... (md)
Characiformes
Astyanax fasciatus ..... (md)
Stomiiformes
Argyropelecus pacificus ..... (cs, md)
Chauliodus macouni ..... (md)
Diplophos taenia ..... (cs, md)
Tactostoma macropus ..... (cs, md)
Vinciguerria nimbaria ..... (cs, md)
Aulopiformes
Aulopus filamentosus ..... (md)
Chlorophthalmus agassizi ..... (cs)
• *Nematonotus* sp. ..... (f)
Saurida tumbil ..... (csb)
Synodus foetens ..... (md)
S. saurus ..... (md)
S. synodus ..... (cs)
Myctophiformes
Myctophum sp. ..... (cs, md)
Protomyctophum thompsoni ..... (cs, md)
Stenobrachius leucopsarus ..... (md)
Symbolophorus sp. ..... (cs, md)
Percopsiformes
Chologaster agassizi ..... (md)
Percopsis omiscomaycus ..... (cs, md)
• *Tricophanes foliarum* ..... (f)
unidentified percopsid fossils ..... (f)
Gadiformes
Lota lota ..... (ds, md)
Microgadus proximus ..... (md)
Batrachoidiformes
Porichthys notatus ..... (csb)
Cyprinodontiformes
Fundulus diaphanus ..... (cs)
Xiphophorus maculatus ..... (cs)
Atheriniformes
Hypoatherina (= Allanetta) harringtonensis ..... (md)
Menidia menidia ..... (cs)
Stephanoberyciformes
Melamphaes lugubris ..... (md)
Beryciformes
Plectrypops retrospinis ..... (cs, md)
Sargocentron (= Adioryx) coruscus ..... (md)
Gasterosteiformes
Gasterosteus aculeatus ..... (csb)
Pungitius platygaster ..... (csb)
Scorpaeniformes
Apistops caloundra ..... (md)
Chitonotus pugetensis ..... (csb)
Cottus cognatus ..... (csb)
Liparis fucensis ..... (md)
Malacocottus kincaidi ..... (csb)
Sebastes ruberrimus ..... (ds)
Perciformes
Caprodon schlegeli ..... (md)
Centropristis striata ..... (md)
Chanda (= Ambassis) sp. ..... (md)
Epinephelus sexfasciatus ..... (md)
Etheostoma blennioides ..... (md)
• *Mioplosus* sp. ..... (f)
Morone americana ..... (csb)
Perca flavescens ..... (csb, md)
• *Priscacara* sp. ..... (f)
• *P. liops* ..... (f)
Stizostedion vitreum ..... (ds)

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Gobryidae, a New Family of Acalyptrate Flies (Diptera: Diopsoidea), and a Discussion of Relationships of the Diopsoid Families

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ABSTRACT. Relationships among families referred to the superfamily Diopsoidea (or Nothyboidea) are discussed from the evidence of comparative morphology, particular attention being given to the Nothybidae, Psilidae, Syringogastridae, and Diopsidae. Some comments are made on selection of autapomorphies in cladistic methodology. The Tanypezidae and Somatiidae are removed from the Diopsoidea to *incertae sedis*. The new diopsoid family Gobryidae, or hinge flies, is established for the Oriental-Australasian genus *Gobrya* Walker, previously variously associated with the families Megamerinidae, Nothybidae, and Syringogastridae. A key to the families which have been included in Diopsoidea is given. A systematic arrangement of taxa mentioned in the discussion is appended.

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The genus *Gobrya* was described by Walker (1860) in the "Subfam. Psilides" of the family Muscidae. Walker's only originally included species of *Gobrya* was *G. bacchoides* Walker, from Celebes, Indonesia (type species by monotypy).

Hendel (1913) treated *Gobrya* and his newly described genus *Syrittomyia* in the "Megamerininae", later raised to family rank as Megamerinidae. He separated *Syrittomyia* from *Gobrya* because of the supposed reduction of the subcosta in the wing of the latter. This, however, was an error, as *Gobrya* consistently has a complete subcosta, and the two names were synonymised by Steyskal (1977). The Megamerinidae have commonly been referred to the superfamily Diopsoidea (subjective synonym Nothyboidea) following Hennig (1958), but D. McAlpine (1997) transferred the Megamerinidae, excluding *Gobrya*, to the Nerioidea.

Gobrya is known from Taiwan, the Philippines, Malaysia, Indonesia, and New Guinea (Steyskal, 1977; and author's observations). Steyskal listed five described species of *Gobrya* (loc. cit.), but has generously supplied me with a copy (dated 1967) of a preliminary manuscript key to seven species, two of them undescribed. I have on hand material of four species, at least one of which is not in Steyskal's key. Hence, there are at least eight species of *Gobrya* in collections. I introduce the common name hinge flies for these insects, in reference to the hinge-like articulation between the thorax and abdomen (compare base of abdomen of *Gobrya*, Fig. 1, with that of *Nothybus*, Fig. 3).

I have collected several specimens of *Gobrya*, including both sexes, on foliage in or at the margin of lowland rainforests in West Malaysia and Papua New Guinea. The immature stages are unknown.

The morphology of *Gobrya* is largely undescribed, and it is the aim of this paper to make known aspects of the adult morphology of this genus, together with that of other taxa that have been referred to the superfamily Diopsoidea or Nothyboidea, in order to throw some light on its phylogenetic relationships.

Morphological terms here used are explained by Colless & D. McAlpine (1991), D. McAlpine (1973), and Harrison (1959). I have tended, where possible, to use traditional terms in preference to terms that suggest doubtful, disputed, or imprecise homologies. Authors of all genera mentioned are given in Table 2.

Notes on cladistic methods

In my discussions of classification systems I have rarely mentioned work published before that of Hennig (1958), because this work, which initiated a modern cladistic approach to classification of Schizophora, superseded nearly everything previously published on the subject. On the other hand, conclusions reached by Hennig in that paper have often subsequently been revised, both by Hennig and other dipterists.

My own treatment of the comparative data does not always lead to the formulation of detailed cladistic hypotheses. Because it is intrinsically improbable that the available morphological data are adequate for or relevant to answering every question in cladistic reconstruction (D. McAlpine, 1996), one should not feel forced to produce a solution to the relationships of every taxon, e.g., by identification of its sister group. I have, however, often indicated where an existing hypothesis rests on a basis which I consider to be scientifically inadequate.

In cladistic analysis, I consider it necessary to apply stringent criteria for the selection of autapomorphies to be cited as the primal evidence for postulating monophyletic taxa. The most reliable apomorphies for this purpose possess the qualities of infrequent arisal, a degree of complexity, and relative stability, as indicated by a broad study of related taxa. An apomorphic character state which does not go some way to meeting these criteria, while not providing primal evidence for monophyly of a taxon, may sometimes be deduced to be an autapomorphy of the taxon as a corollary to a theory of monophyly. If secondarily deduced autapomorphies are added to lists of autapomorphies for a hypothetically monophyletic taxon, their inclusion in the evidence for its monophyly leads to circular reasoning and an unjustified degree of confidence in the cladistic hypothesis. The above distinctions are made because of numbers of difficulties with cladistic logic encountered in the literature on higher Diptera. It sometimes appears, where studies have included lists of secondarily deduced autapomorphies in accordance with a particular cladistic hypothesis, that an alternative cladistic hypothesis could be made to appear equally credible simply by reversing the polarities of selected character sequences (i.e. rededucing them to fit another hypothesis).

The superfamily Diopsoidea (syn. Nothyboidea)

The Nothybidae and Psilidae

Aczél (1955) placed the Nothybidae in a separate superfamily, Nothyboidea, from all other Schizophora, because he thought it was the only schizophoran group with the male postabdomen symmetrical and therefore not circumverted. In this he was mistaken, for in many schizophoran families the male postabdomen (particularly in the more or less reduced protandrial segments 6–8) is symmetrical (e.g., Conopidae, Drosophilidae, Ephydridae, Lauxaniidae, Psilidae, Teratomyzidae, etc.). The Dolichopodidae, in which the protandrium possesses groundplan asymmetry, includes also forms with secondary symmetry (D. Bickel, pers. comm.). This is no longer taken as evidence of lack of circumversion of the genital segment, at least historically, in these taxa (see Hennig, 1958; Griffiths, 1972).

Hennig (1958) employed the superfamily Nothyboidea to include the families Diopsidae, Nothybidae, Megamerinidae, Tanypezidae, Strongylophthalmyiidae, and Psilidae, although he was unable to find a single apomorphy to establish monophyly of the superfamily. J. McAlpine (1989) recognised the same superfamily concept as Diopsoidea (on grounds of nomenclatural priority), with the addition of Somatiidae and Syringogastridae. J. McAlpine (1989) considered the Diopsoidea and Nerioidea to be sister groups, but I have found no validity in the evidence presented (D. McAlpine, 1996).

Griffiths (1972) used a revised concept of the Nothyboidea to include only the families Nothybidae, Psilidae, Teratomyzidae, and Periscelididae (the last including *Somatia* but not *Cyamops* and *Stenomicra*). I do not find the four stated groundplan apomorphies at all convincing as support for his superfamily concept. Among such a diverse lot of taxa, only unusually distinctive apomorphies can provide acceptable evidence for interrelationships, and these four are very widely distributed among acalyptrate families and undoubtedly subject to convergence.

Griffiths also suggested, but simultaneously queried, a sister group relationship between Nothybidae and Teratomyzidae (1972, fig. 16, and accompanying table), supported by the following three apomorphies (from his more extensive listing for nothyboid families): 1, postvertical bristles reduced; 5, axillary lobe and alula reduced; 7, lower basal cell (bm) open anterodistally. These do not appear to provide a set of primal synapomorphies, because the postvertical bristles, though absent in Nothybidae, are well developed but rather short in the groundplan of Teratomyzidae; the alula is not as much reduced in the groundplan of Teratomyzidae as it is in many other taxa of elongate acalyptrate flies; the cell bm is not open anterodistally in the Teratomyzidae, but

vein 4 has a flexure or weak point in this region. I find such a weakening or flexure in the basal section of vein 4 to be manifested to a variable degree in some taxa of Agromyzidae, Coelopidae, Heleomyzidae, Helosciomyzidae, Pallopteridae, Platystomatidae, Psilidae, Sepsidae, Tephritidae, and Tethinidae. The Teratomyzidae, which have been the subject of a recent study (D. McAlpine & de Keyzer, 1994), are widely different from the Nothybidae in their morphology, except for the simplified, symmetrical protandrium; also the aedeagal characters, which Griffiths considered significant for placement in the Nothyboidea, are quite diverse among the teratomyzids and their groundplan conditions for the family are uncertain. I consider that there is no case for considering the Nothybidae and Teratomyzidae to be closely related.

The Nothybidae and Psilidae show some interesting points of morphological resemblance. There is an enlarged postocular bristle laterad of the outer vertical in *Nothybus* and in several psilid genera (so that it may be present in the groundplan of both families). There are, however, some difficulties in establishing homologies of bristles on the upper part of the head in both families, as indicated by Hennig (1958). There is a general resemblance in antennal structure between Nothybidae and Psilidae, but a more detailed resemblance between Nothybidae and *Gobrya*, as indicated below. The anterior notopleural bristle is absent in Nothybidae and Psilidae, as in many other elongate flies (see D. McAlpine, 1997). The apparent groundplan for both Nothybidae and Psilidae includes a secondarily symmetrical male abdominal segment 6 with ventrally placed sternite. The groundplan for both families probably includes a largely membranous distiphallus which is ribbon-like and almost symmetrical.

The most likely synapomorphies for Nothybidae and Psilidae would seem to be in the male postabdominal conditions indicated, the subcircular prothoracic spiracle not largely closed over by intermeshed hairs on its outer lips, and the enlarged postocular bristle. As indications of relationship these seem to conflict with the evidence for relationship between *Gobrya* and Nothybidae reviewed below.

Some of the numerous character states of Nothybidae which differ from those of Psilidae (the latter bracketed) are as follows: (1) distal articular surface of antennal segment 2 facing forwards (facing downwards); (2) lateral arms of ptilinal fissure much abbreviated (moderately long and decurrent on parafacial); (3) prothoracic precoxal bridge extremely broad (absent); (4) subscutellum hypertrophied (not prominent, sometimes vestigial); (5) mesopleural bristle present (absent); (6) pleurotergite setulose, without noticeable pubescence (pubescent, without setulae); (7) tibiae with setulae all aligned in several longitudinal series (tibial setulae irregularly placed); (8) subcosta completely sclerotised distally, terminating in costa close to termination of vein 1 (subcosta desclerotised distally, terminating well before end of vein 1); (9) first and second basal cells partly confluent (completely separated); (10) alula absent (present); (11) female with spermathecal vesicles (spermathecal vesicles absent, ?consistently). In many of these characters the Nothybid state is apomorphic relative to the psilid state, but the psilids are apomorphic in characters 8 (at least partly) and 11. In characters 1, 5, and 6, polarity is uncertain, and, if Nothybidae and Psilidae are not sister-groups, it may not be reasonable to regard a character state present in one family as necessarily directly derived from that of the other.

An intriguing possibility, which I cannot at present regard as a probability, is the following: the Nothybidae are not closely related to any of the families here placed in the Diopsoidea, but are derived from near the Curtonotidae in the superfamily Ephydroidea (syn. Drosophiloidea). Because I cannot completely refute this idea, I point out some evidence for and against it. The Curtonotidae are considered to include the genera *Curtonotum*, *Cyrtona*, and *Axinota*. The following 13 conditions (a–m) could be considered to give some support to this hypothesis.

(a) The antennal structure of Nothybidae, described above, agrees with that of *Curtonotum* in most details, as it does with most diopsoids (other than Diopsidae).

(b) In Nothybidae and Curtonotidae the external opening of the prothoracic spiracle is subcircular, instead of having the usual narrowly two-lipped conformation. This feature does not, however, give a separation from Psilidae, as mentioned above.

(c) The scutellum in Nothybidae has two pairs of large bristles on its margins. This agrees with Curtonotidae and most other ephydroid taxa, but in the typical diopsoid taxa there is only one large pair of scutellar bristles, the apical pair, and any others are much smaller.

(d) While Nothybidae are noted for the prominently hypertrophied subscutellum, that of *Curtonotum* more nearly approaches the nothybid condition than any other taxon included in the Diopsoidea.

(e) The presence of a mesopleural bristle in Nothybidae is in disagreement with other taxa here placed in Diopsoidea, but one or two mesopleurals are present in many taxa of Ephydroidea, including the Curtonotidae, but not the Drosophilidae. A mesopleural bristle is so widely present among schizophoran taxa, that its presence does not constitute a very particular point of agreement for the above families.

(f) The setulae on the tibiae in Nothybidae and Curtonotidae are arranged in longitudinal rows, a condition present in many other ephydroids. However, this character does not give a good separation from other taxa of Diopsoidea, many of which show a tendency for these setulae to become seriate.

(g) The tarsi of Curtonotidae (least so in *Cyrtona*) are, like those of Nothybidae, remarkably long, slender and subcylindrical. In most other diopsoids the tarsi are either somewhat shorter, in relation to the tibiae, or somewhat more depressed.

(h) The subcosta in Nothybidae, as in *Curtonotum*, is fully developed to its distal termination in the costa very near but quite separate from the end of vein 1. The variations in subcostal development in other diopsoid

taxa do not include these precise features.

(i) In both the Nothybidae and Curtonotidae the anal region of the wing, immediately beyond the alular region, is narrowed, the margin here showing more or less concave curvature, and the much shortened but sclerotised distal section of vein 6 ends at or near the margin. Although basal wing-narrowing occurs in other diopsoid families, it does not follow this pattern. I note here that J. McAlpine (1989) was mistaken in considering vein 7 (A_2) to be visible in this region in both Curtonotidae and Cryptochetidae. The correct identities of the anal veins in these flies, as given by Hennig (1958), become apparent when the curtonotid genera are carefully compared with the less reduced forms of Drosophilidae. The structure in *Cyrtona* illustrates the true position of vein 6 and also shows how a secondary spur is liable to misidentification as vein 6 in the Cryptochetidae. I affirm that there is no trace of vein 7 beyond the alular region in any taxon of either Diopsoidea or Ephydroidea.

(j) In both Nothybidae and Curtonotidae there is a convex longitudinal crease of the wing membrane arising just beyond the origin of the distal section of vein 6. This crease is not the homologue of any true vein, and is not known to me in other taxa of Diopsoidea, though there is a trace of it in a few other ephydroid taxa, e.g., Diastatidae.

(k) In the male postabdomen of Nothybidae and Curtonotidae there is a somewhat similar degree of reduction of sclerites of segments 6 to 8, in contrast to the large tergite and sternite 5, with a tendency towards symmetry.

(l) The male genital segment of Nothybidae and Curtonotidae is directed posteriorly, in contrast to that of most taxa of Diopsoidea and Ephydroidea, in which the genital segment is directed ventrally. In the diopsoid family Psilidae there is also a strong tendency for the genital segment to be directed posteriorly.

(m) Pollock (1996) has recorded ovoviviparity in the curtonotid *Cyrtona*, a condition which it shares with *Nothybus longithorax* Rondani. This is apparently an infrequently derived condition in acalyptrate taxa, the few other known cases being listed by Pollock. However, it is not known if it is a groundplan condition for either Nothybidae or Curtonotidae.

Of the above arguments, (a), (b), (f), (k), (l), (m) may be seen as rendering relationships of Nothybidae to Ephydroidea as feasible as to Diopsoidea, while (c), (d), (e), (g), (h), (i), (j) may, to varying degrees, be seen as favouring the hypothesis of ephydroid relationships (with particular reference to the Curtonotidae) over that of diopsoid relationships.

The above indications of possible relationship between Nothybidae and Curtonotidae seem to be countered by the following points, (n) to (s), which are more in accordance with diopsoid relationships for the Nothybidae.

(n) The Nothybidae lack the postvertical bristle, vibrissa, and seriate postocular setulae, as in *Gobrya*, Syringogastridae, and Diopsidae. Such a degree of reduction of cephalic bristles is unusual in the Ephydroidea and not found in the Curtonotidae.

(o) The Nothybidae lack the humeral, anterior notopleural, presutural, and sternopleural bristles. This reduction of thoracic bristles is in disagreement with Curtonotidae and most less reduced ephydroids, but is typical of the Diopsoidea.

(p) The Nothybidae lack the preapical dorsal tibial bristle, characteristic of the Curtonotidae, Diastatidae and many drosophilids, but uniformly absent in Diopsoidea.

(q) The costa in Nothybidae lacks the break at the subcostal position. This condition disagrees with probably all macropterous Ephydroidea, but agrees with the diopsoid taxa other than Psilidae.

(r) In the Nothybidae the basal end of the discal cell is strongly enclosed, but the second basal cell is confluent with the first basal cell because of an extensive break in vein 4. This condition contrasts with that in Curtonotidae, where vein 4 is complete but the basal end of the discal cell is confluent with the second basal cell. In those ephydroids with discal and second basal cells visibly separated, the basal crossvein separating them is generally weakly sclerotised. This difference between Nothybidae and typical ephydroids is most readily explained as an independent derivation of each condition from a plesiomorphic condition with both basal cells completely enclosed by well sclerotised veins, as in the Psilidae. A similar pattern of variation in these cells at a lower taxonomic level occurs in the family Neurochaetidae, where the two different apomorphic conditions distinguishing the genera *Neurotexis* and *Neurochaeta* have been separately derived from the plesiomorphic condition found in *Anthoclusia* and *Neurocytta* (D. McAlpine, 1993).

(s) the Nothybidae lack the incomplete suture between abdominal tergites 1 and 2, present in the Curtonotidae and other less reduced forms of Ephydroidea. This suture is absent in all typical families of Diopsoidea.

For the above reasons I leave the Nothybidae in the provisional superfamily Diopsoidea. The problem of relationships between Nothybidae and *Gobrya* will be discussed below.

The Syringogastridae and Diopsidae

The neotropical genus *Syringogaster* was generally placed in the Megamerinidae until Prado (1969) erected for it the family Syringogastridae in a detailed taxonomic review. Griffiths (1972) regarded the Syringogastridae as the sister group of the Diopsidae (including Centrioncinae), the two families together forming his "prefamily Diopsoinea". J. McAlpine (1989) accepted family status for Syringogastridae, but placed it as a sister group of Megamerinidae (including *Gobrya*), a classification I consider too improbable for further consideration (see D. McAlpine, 1997).

I accept that Syringogastridae and Diopsidae (including Centrioncinae) are sister groups on the basis of a different set of synapomorphies from those

given by Griffiths. I review the eight autapomorphies listed by Griffiths (1972) in support of monophyly of the Diopsoinea as follows, drawing comparisons with other families (numbering as given by Griffiths except that characters (2) and (4) are separated into their components):

(1) *Postvertical bristles absent.* This is an apomorphy relative to the plesiomorphic state of Psilidae, but, because the apomorphic state is present in the groundplan of outgroups Nothybidae and *Gobrya*, it cannot be claimed as a primal autapomorphy for Diopsoinea (synapomorphy for Syringogastridae and Diopsidae *sensu* Hennig, 1965).

(2a) *Only one fronto-orbital (ors)... present.* This is perhaps an apomorphy relative to the presence of two pairs of fronto-orbital bristles, which is perhaps a groundplan plesiomorphy for the Psilidae. The outgroup Nothybidae is subject to interpretation as having one, two, or three fronto-orbitals. Doubt as to whether the foremost frontal bristle of Nothybidae is the homologue of a fronto-orbital (supraorbital) bristle arises from its unusual position, but the doubtfully inferred presence of three fronto-orbitals (Hennig, 1958: fig. 54) seems not to rest on any firm evidence. *Syringogaster* has no fronto-orbital bristles, like *Gobrya*, but there is no evidence as to whether the condition in the former was attained by loss of a single such bristle or by simultaneous reduction of two bristles. For these reasons I am doubtful if the inferred presence of one pair of fronto-orbitals in the groundplan of Diopsoinea is an autapomorphy.

(2b) *Only... one vertical bristle (vte) present.* This could be a valid autapomorphy, though its interpretation is disputed by Feijen (1989) on improbable grounds.

(3) *Only one postalar bristle present.* As this condition is present in the outgroups Nothybidae, Psilidae, and *Gobrya*, it cannot be claimed as a primal autapomorphy for Diopsoinea.

(4a) *First and second abdominal terga fused, forming syntergum which is the largest sclerite of the abdomen.* Partial fusion of tergites 1 and 2 is evidently present in the groundplan of the Schizophora. As complete fusion is present in all likely diopsoid outgroups (Somatiidae excluded) this cannot be claimed as an autapomorphy for Diopsoinea.

(4b) *Basal segments of abdomen (especially the second segment) elongate, but distal segments becoming short and wide, so that the abdomen has a petiolate appearance.* This condition is present in the outgroup *Gobrya* and to a varying extent in many elongate acalyptrate flies of various families. In several primitive diopsid genera the condition is only slightly developed. Hence its status as an autapomorphy for Diopsoinea is unconvincing.

(5) *Seventh sternum (male) forming complete ventral band of sclerotisation, fused with inverted eighth sternum on right side...* This may be a genuine autapomorphy but it needs more investigation within the Diopsidae where sternite 7 is variable. The fusion of a ventrally placed sternite 7 with sternite 8 on the right side does not occur in outgroups.

(6) *Seventh and eighth tergum vestiges (male) lost.* This is the condition in all diopsoid families and most other families of Schizophora. It is therefore illogical to give it as an autapomorphy for Diopsoinea.

(7) *Seventh left spiracle (male) lying within seventh sternum.* While this condition may be in the groundplan of Diopsoinea, its presence in *Gobrya*, which otherwise has a rather different protandrium (Fig. 8), precludes its recognition as a primal autapomorphy for Diopsoinea.

(8) *Aedeagus (male) rather short, with a complex distal section which bears lobes or processes.* There is a strong resemblance between the aedeagi of *Syringogaster* and certain diopsids (compare figs 79 and 80 of Griffiths, 1972, and the figures of *Sphyracephala* spp. of Feijen, 1989), even though homology of individual lobes has not been demonstrated. This condition, according to the above general description, occurs also in *Gobrya* (Fig. 12), but not in the investigated taxa of Nothybidae and Psilidae. The evidence suggests that this condition of the aedeagus may be a synapomorphy for *Gobrya* and Diopsoinea, rather than an autapomorphy for Diopsoinea.

Despite the above arguments, I believe that the taxa constituting Griffiths' Diopsoinea together form a monophyletic group as indicated by the synapomorphies for Syringogastridae and Diopsidae set out in Table 1. Four of these, (a) the presence of a supra-alar carina, (b) the cylindrical extension of metathorax, (c) the presence of tarsal sawlines, and (d) the reduction of the inner vertical bristles (together with general cephalic chaetotaxy) call for special comment.

(a) The supra-alar carina (Figs 34–36) is a structure which, within my experience, is peculiar to the Syringogastridae and Diopsidae. It is probably at its most primitive condition in *Centrioncus* (including *Teloglabrus*, Fig. 35), where it consists of a well-defined ridge on the surface of the mesoscutum passing posterodorsally from the postnotopleural ridge (as defined by D. McAlpine, 1991: 32–33) to the base of the supra-alar bristle. In the Syringogastridae and most Diopsinae the supra-alar bristle is vestigial or absent (probably as a convergent apomorphy in the two groups), but the carina remains. In the Diopsinae (sensu Hennig), other than the *Teleopsis* complex (Fig. 36), the supra-alar carina is more extended posteriorly than in the Syringogastridae, so that in these forms which possess a supra-alar bristle (or a secondary hair at the summit of the carina) it lies only slightly in advance of the dorsomedially displaced postalar bristle.

In the genus *Teleopsis* the summit of the supra-alar carina is produced as a large spinous process (the supra-alar spine) and the lower part of the carina is more or less obsolete. This highly apomorphic condition is the only modification known to me in the Diopsoinea involving significant reduction of the supra-alar carina. The supra-alar carina is a quite distinct development from the horizontal lamina formed by the postnotopleural ridge in the Megamerinidae, some Coelopidae (genus *Coelopa*, see D. McAlpine 1991, fig. 7), Curtonotidae (especially *Curtonotum*), some Psilidae (genus *Loxocera*),

and some Platystomatidae (e.g., genus *Giraffomyia*).

(b) The cylindrical posterior extension of the metathorax is found only in the Diopsoinea among the taxa of Diopsoidea and is usually quite short (Figs 38, 39). As a prerequisite to the cylindrical extension, there must be a well sclerotised metathoracic postcoxal bridge to provide support for its lower part. Such a postcoxal bridge is present in all available taxa of Diopsoinea, as in a number of other schizophoran taxa. The upper part of the cylindrical extension is developed from the margin of the metanotum, a sclerite which occurs in most schizophorans as an inconspicuous transversely attenuated rim on the posterior margin of the postscutellum. In the Diopsoinea the metanotum is always somewhat better developed, and in *Syringogaster papaveroi* Prado it is remarkably large (Fig. 38). A cylindrical extension of the metathorax similar to that of the Diopsoinea occurs in the platystomatid subfamily Angitulinae.

(c) A tarsal sawline consists of a well defined linear longitudinal series of short, compressed cuneate setulae situated on either the anterior or posterior side of a tarsal segment. The sawline is well differentiated from any other longitudinal series of tarsal setulae, its component setulae being typically shorter and more closely placed, so that it may look like a continuous line under low magnification (Fig. 40). Its setulae usually consist of two kinds, which alternate along its length (Figs 41–43), the larger being longitudinally grooved with the basal socket usually evident, the smaller being almost smooth, arising at a different angle to the larger ones, and without evident basal sockets. However, it should be remembered that the electron micrographs may sometimes fail to show existing basal sockets as they do not indicate more transparent zones of cuticle. Often a larger setula and its distally adjacent smaller setula are set on a common basal prominence as in Fig. 43.

A sawline is present on the mid basitarsus (mid tarsal segment 1) of all diopsids examined except *Sphyracephala (Sphyracephala) brevicornis* (Say) and even in the latter there is a loose posterior series of less specialised setulae which are probably homologous with the sawline of other genera. In *Sphyracephala (Hexechopsis) beccarii* (Rondani) the sawline is identifiable on the posterior surfaces of mid tarsal segments 1 and 2, but is somewhat atypical in consisting of longer, less crowded setulae than in most diopsids. *Sphyracephala* and *Pseudodiopsis* differ from other diopsids in the absence of sawlines on the hind tarsus, whereas other genera examined have at least the anterior side of hind tarsal segment 1 with a sawline, except *Centrioncus*, which has well developed sawlines only on the posterior surfaces of hind tarsal segments 1–4. A sawline is present on the fore tarsus (posterior surface of segment 1 only) only in the advanced diopsine genera (e.g., *Diasemopsis, Cyrtodiopsis, Teleopsis*, and *Diopsis*). In *Centrioncus* well developed sawlines are present on the posterior surfaces of mid tarsal segments 1–4 and also extend for most of the length of the mid tibia on the posterior surface.

In the two presently available somewhat morphologically divergent species of *Syringogaster* (*S. papaveroi* Prado, Brazil, and *Syringogaster* sp., Costa Rica, see Fig. 40), both anterior and posterior sawlines are present on segments 1–4 of the mid tarsus and anterior ones on the hind tarsus in both sexes, but sawlines are absent from the fore tarsus.

From the distribution of tarsal sawlines in diopsids it can only be confidently stated that the groundplan for the family includes the presence of a posterior sawline on mid tarsal segment 1. There is a possibility, however, that the groundplan includes a more extensive presence of tarsal sawlines, and, in view of their presence in Syringogastridae, Centrioncinae, and Diopsinae, the reduction of sawlines in *Sphyracephala* is apparently a derived state.

In a non-exhaustive survey of cyclorrhaphous families I have found tarsal structures resembling diopsid sawlines to a varying extent only in the Platypezoidea (syn. Phoroidea; families Ironomyiidae, Sciadoceridae, Phoridae, Platypezidae, but not Lonchopteridae; Opetiidae not examined), certain Ephydroidea (syn. Drosophiloidea sensu Hennig, 1958), and in the Glossinidae (superfamily Muscoidea = Calyptrata). The survey revealed some diversity in setation and spination of the tarsi. In some groups there are very loose series of spaced spines. In others the setulae of the basitarsus have a tendency to form several longitudinal series, most conspicuous in Neriidae, Nothybidae, and some calyptrates, but, outside the previously mentioned groups, none shows such a distinct, dense, anterior and posterior series as do the Diopsidae and Syringogastridae.

In the Ephydroidea typical basitarsal sawlines occur apparently only in the Curtonotidae and a number of genera of Drosophilidae. In the Drosophilidae they are not restricted, as has been sometimes supposed, to the subfamily Steganinae but occur also in some species of *Drosophila* (Castro, 1953, and author's observations). They commonly consist of two kinds of processes alternating in each series, as in the Diopsoinea. The tarsal sex-combs present in males of some *Drosophila* species are quite different from sawlines. Other ephydroids (e.g., Diastatidae, Camillidae) have loose longitudinal combs of setulae on the basitarsi, but no sawlines.

The distribution of presence of tarsal sawlines in the Cyclorrhapha suggests that their presence is an apomorphy of infrequent arisal, having probably arisen as few as three times in the Schizophora. Their presence in the groundplans of Diopsidae and Syringogastridae is significant evidence for the monophyly of the Diopsoinea and emphasises its morphological distance from other diopsoid groups.

(d) The genera *Diopsina* and *Cyrtodiopsis* include several remarkably hirsute diopsid species (some well illustrated by Feijen, 1981), having many long setulae on the head, legs, scutellum, and other parts of the thorax and abdomen, some of those on the head and thorax tending to a symmetrical arrangement. Also, in *Pseudodiopsis* there is a linear fringe of setulae on the frontal orbits. In many taxa of Schizophora there are

minor setulae on the orbital plates and elsewhere on the head, but these, for the most part, do not intergrade with true fronto-orbital bristles. In those diopsids with setulae or hairs on the ocellar tubercle their size is similar to and dependent on that of the other frontal setulae, and in *Cyrtodiopsis* they show the same modified apices. However, Feijen (1983) supposes that those setulae which appear to be in the position of ocellar and fronto-orbital bristles are in fact the homologues of these bristles in other dipterous families. On this basis he attributes the presence of a pair of ocellar bristles and of "several" fronto-orbital bristles to the groundplan of both the Diopsoinea and the "Diopsidae" (s.str., i.e. the subfamily Diopsinae of Hennig, 1965), and declines to recognise the two really distinct pairs of cephalic bristles present in many diopsines as homologous with the two pairs present in centrioncines. The two pairs of cephalic bristles present in the groundplan of the Diopsidae are most logically treated as outer vertical (vte) and fronto-orbital (ors) bristles as indicated by Hennig (1965: figs. 45, 46). Also, it can be stated that, in the groundplan of the Diopsidae, the ocellar bristles are undifferentiated from frontal setulae, though well differentiated proclinate, divergent ocellar bristles are present in the groundplan of Syringogastridae. As the ocellar bristles of Syringogastridae appear to be homologous with those of Psilidae and more remote outgroups, it is probable that their presence is a groundplan plesiomorphy for the Diopsoinea.

In addition to the autapomorphies for the Diopsoinea given in Table 1, the presence of densely microtrichose crazed cuticle on the face is almost certainly a groundplan condition for Diopsoinea, and may be an autapomorphy. It is present, with some variation, in *Centrioncus, Sphyracephala*, and *Syringogaster* (Figs 20, 22, 24), i.e. in all major clades of Diopsoinea, or at least in their more "basal" taxa (*Sphyracephala* being a remarkably primitive genus of Diopsinae). The crazed appearance of this cuticle is produced by numerous fine but apparently deep suture-like grooves, with a mainly almost vertical orientation. Some of the grooves appear to widen in an irregular manner, probably through shrinkage of the cuticle in drying. The grooves divide the surface of the cuticle into many vertically elongate plates, most of which bear a single microtrichium each. The scale-like structures on the face of *Syringogaster* are homologised with microtrichia, or at least with their dilated bases, because of their similarity to the facial microtrichia of *Centrioncus* (compare Figs 20, 22).

Because of lack of knowledge of ultrastructure of the face in other acalyptrate families, I hesitate to class the presence of densely microtrichose crazed cuticle on the face as a definite autapomorphy of the Diopsoinea, though it may be so.

The parafacial of *Centrioncus, Sphyracephala*, and *Syringogaster* has a dense covering of "pubescence", in the first two of similar size to that on the face. However, these parafacial hair-elements differ from those on the face in being wholly or partly socket-based macrotrichia (Fig. 23). (Electron microscopy does not always enable ready discrimination of macrotrichia from microtrichia as the membranous rings surrounding the bases of the former are distinguishable only if somewhat sunken). I therefore regard the presence of dense, minute parafacial macrotrichia as a groundplan condition of Diopsoinea, but I cannot determine if it is an autapomorphy for Diopsoinea, because it has not yet been demonstrated if the condition is also present in outgroups.

The absence of any dorsocentral bristle is a groundplan apomorphy for the Diopsoinea, judging from the universal absence of such a bristle among the included taxa. I do not, however, treat the condition as an autapomorphy, as it is shared with the outgroup *Gobrya*. Presence of a dorsocentral has been claimed for some diopsids, but this is an error. The large bristle that looks like a dorsocentral in some taxa (e.g., in fig. 61.1 of Peterson, 1987) is the medially displaced postalar bristle, as discussed below.

The pitting along the median ventral suture of the sternopleura in some taxa of Diopsoinea shows some interesting diversity. In *Syringogaster* sp. (Fig. 26), there is a single median series of relatively few, spaced, deep pits, of which the foremost is the largest. The suture is apparent as a dark internal line (therefore not visible in the electron micrograph). The condition in *Centrioncus* spp. is very similar, but the pits are more numerous and crowded. In most Diopsinae the median sternopleural suture is externally apparent as a groove or ridge, sometimes as a narrow ridge lying within a groove. In most diopsine taxa there are no pits associated with this suture, but in *Sphyracephala* sp. (Fig. 27), a somewhat primitive diopsine, there is a series of pits on each side of a slight median ridge.

A possible evolutionary sequence for these structures is as follows. The uniform median groove, representing the median ventral suture in such outgroups as the Psilidae, has become sunken in such a way that it is represented on the surface only by a series of pits (as in *Syringogaster* and *Centrioncus*). A further strengthening of the suture brought about emergence of the suture as a surface ridge dividing the originally uniseriate pits in two (as in *Sphyracephala*) . Further modification of the thorax brought about loss of the pits (as in *Cyrtodiopsis*, *Diopsis* etc). In *Gobrya cyanea* there is weak transverse rugosity on the posteroventral parts of the sternopleura (Fig. 25); but this condition cannot form part of the above series, as *Gobrya* lies outside the Diopsoinea phylogenetically.

Because the above sequence is inferred partly from a particular interpretation of phylogeny within the Diopsoinea, it cannot be classed as primal evidence for inferring phylogenetic relationships among the included taxa. It is reasonably certain from their taxonomic distribution that median sternopleural pits occur in some form in the groundplan of the Diopsoinea. Because what appear to be rudimentary sternopleural pits occur in *Gobrya*, I do not list the presence of these pits as an autapomorphy of Diopsoinea.

The assertions of Feijen (1983; 1989), that the (probably upper Eocene) fossil *Prosphyracephala* was

a true sphyracephaline contemporary with true diopsines, and that Syringogastridae and Centrioncinae (Centrioncidae in Feijen's classification) are sister groups which separated from each other before the end of the Cretaceous, do not arise from a logical treatment of the available data. In my view, the primary groupings of Diopsidae given by Hennig (1965) are more likely to be phylogenetically valid than either those of Feijen or those of Steyskal (1972).

The family Syringogastridae was well characterised by Prado (1969) and treated as a monophyletic group by Griffiths (1972). J. McAlpine (1989: table 116.2) gave several autapomorphies for the Syringogastridae, but unfortunately treated the remotely related Megamerinidae as the relevant outgroup. Therefore the majority of given character states, though apomorphic in the broader field, are not autapomorphies for Syringogastridae. The following four conditions (a–d) would appear to be distinctive syringogastrid autapomorphies, if they can be confirmed for more species than are at present available to me.

(a) *Pleurotergite, without convex callus*. In outgroups of various levels in the Schizophora there is a convex callus on the pleurotergite, which, in the Diopsinae, bears a cuticular spine, unfortunately termed "metapleural spine" by Feijen (1983).

(b) *Anterior margin of metathoracic spiracle with blunt cuticular spine* (Fig, 29). This is a distinctive syringogastrid condition, not encountered in outgroups.

(c) *Median panel of face with dense covering of scales* (Figs 19, 20). These are probably modified microtrichia (pruinescence) as suggested by comparison with the corresponding surface in *Centrioncus* (Fig. 22), but I have not encountered a similar facial vestiture in my limited studies of other flies under the scanning electron microscope.

(d) *Subscutellum vestigial* (Fig. 31). In most taxa of Diopsoidea there is a distinguishable subscutellum between the scutellum and postscutellum, which forms a convexity separate from that of the latter. A convex subscutellum of variable size is present in the Diopsidae and in *Gobrya* (Fig. 30), but in the available syringogastrids it can be detected only as a linear rim on the dorsal margin of the postscutellum bordering the subscutellar membrane.

As the family Syringogastridae includes a single genus, *Syringogaster*, of limited morphological diversity (Prado, 1969), its monophyletic status seems very probable, though I cannot yet prove that all the above conditions are in its groundplan.

The family Diopsidae has been characterised as a monophyletic group by Hennig (1958) and Griffiths (1972). Because some of the character states given as evidence for monophyly, particularly in the list of Hennig, are not demonstrably groundplan autapomorphies for Diopsidae, I would base my argument for monophyly principally on the following six autapomorphies (a–f).

(a) *Antenna porrect; segment 2 not cap-like, without dorsal slit or seam; segment 3 short, not deflexed, without dorsobasal process fitting into cavity of segment 2, with aristal insertion not closer to basal than to distal extremity* (see Feijen, 1983: figs 4–6). The antenna of Syringogastridae (Figs 17, 18) has much the same complex structure as that of the Psilidae as described below among groundplan characters of Diopsoidea. Also, the arista is bipectinate. These features, with the possible exception of the bipectinate condition of the arista, which is variable in the Psilidae though a consistent condition of Nothybidae and *Gobrya*, are plesiomorphic compared with the contrasting features of the Diopsidae, in which the antenna has more simplified articulation between segments 2 and 3, and more nearly dorsoventrally symmetrical segment 3.

Feijen has reversed the evolutionary polarity of most of these antennal features in the Diopsoinea so far as he has described them, but it must be pointed out that the condition in the most acceptable outgroups to the Diopsoinea is similar to that of Syringogastridae. The strongly dorsoventrally asymmetrical segment 3 with arista inserted dorsally well before mid-length, is very probably a groundplan condition of the Schizophora (and perhaps a synapomorphy for Syrphoidea and Schizophora, Cumming et al. 1995). The condition present (to variable degrees) in typical representatives of the Pseudopomyzidae, Neriidae, Clusiidae, and Diopsinae is almost certainly apomorphic.

(b) *Postalar bristle displaced dorsomedially* (Fig. 35). The Syringogastridae retain the probably plesiomorphic position of the postalar bristle on the lateral surface of the mesoscutum, no higher than the summit of the supra-alar carina (Fig. 34), as in the outgroups Psilidae, Nothybidae, and *Gobrya*. In the Diopsidae the postalar bristle has moved to a more dorsomedial position and in some taxa has subsequently lost its distinction from the mesoscutal setulae (as in Fig. 36). The degree of displacement of the postalar in *Centrioncus*, though quite noticeable, is less extreme than in other diopsids (subfamily Diopsinae).

(c) *Sockets of major pair of scutellar bristles situated at apices of elongate horn-like processes*. This condition is present in all taxa of Diopsidae, but is absent in all out-groups (e.g., Syringogastridae, *Gobrya*, Figs 30, 31). Setiferous scutellar horns have arisen independently in several families of Schizophora (e.g., Chloropidae, Ephydridae), but only in the platystomatid subfamily (? or tribe) Angitulinae do they closely resemble those of Diopsidae. This is interesting, because the Angitulinae are also convergent with Diopsoinea in metathoracic structure and the nature of the articulation between thorax and abdomen.

(d) *Fore coxa and femur enlarged (fore leg raptorial)*. This condition in the Diopsidae is accompanied by the presence of short, incrassate, seriate ventral fore femoral bristles of variable distribution. Such bristles are present in outgroups of two different degrees of removal, viz. Syringogastridae and *Gobrya*, but these groups, as well as all other families of Diopsoidea, lack the enlargement and raptorial modification of the foreleg: hence the deduction that lack of the raptorial modification is the plesiomorphic state for Diopsoinea. Somewhat similar

raptorial enlargement of the foreleg to that of Diopsidae has evolved infrequently in other schizophoran taxa, e.g., in *Ochthera* and *Stratiothyrea* (Ephydridae), *Aragara* (Chloropidae), *Rhinotora* and allied genera (Heleomyzidae), and to a less marked extent in certain sepsids and other taxa.

(e) *Basal crossvein (tb, bm-cu, or base of M_{3+4}) absent.* Among families referred to the Diopsoidea this condition is present only in the Diopsidae. The condition has arisen several times in the Schizophora, mainly in taxa of small body size. Its occurrence is rarer in groups with the size range of Diopsidae, e.g., certain curtonotids, which have probably undergone an increase in size, as evidenced by the smaller body-size in their outgroups.

It is not an aim of this paper to elucidate in detail the internal phylogeny of the Diopsidae, but I note that the characters which are used by Steyskal (1972) and Feijen (1989) to characterise the Sphyracephalini or Sphyracephalinae include no likely apomorphies. *Pseudodiopsis* therefore remains a possibly distinct genus from *Sphyracephala* in my view, as in that of Hennig (1965) and others, because I can find no demonstrable synapomorphies uniting it with *Sphyracephala*. Also, the phylogenetic diagram of Shillito (1971) is not based on principles of Hennigian cladistics.

Feijen (1983) has demonstrated that *Centrioncus* is a polytypic genus, though previously entomologists determined all specimens from many African countries as *C. prodiopsis* Speiser (e.g., Steyskal, 1970a). Feijen has further grouped these *prodiopsis*-like species into two genera, *Centrioncus* s.str. and *Teloglabrus*, though the slight differences given in his key, some of them admittedly inconsistent, would hardly seem to justify generic segregation. However, he states that: "*Centrioncus* [s.str.] are characterized as a monophyletic group by the following groundplan conditions, which are apomorphous with respect to the groundplan of the Centrioncidae: (1) Costal cell partly or wholly glabrous. (2) Subcostal cell absent." These character states are also given in his table 4. I have checked these characters for my available specimens of *Centrioncus* (s.str.) *decoronotus* Feijen and three "*Teloglabrus*" spp. (from South Africa and Zimbabwe, not readily identifiable from Feijen's key). Among the numerous specimens of *C. decoronotus* there is a little variation in the microtrichiation of the costal cells, but the range of variation among the "*Teloglabrus*" spp. is extreme, as indicated in Feijen's own key. These centrioncine flies have a much reduced subcostal cell because of the close proximity of the subcosta to vein 1 over most of its length, and separation of the two veins is best appreciated in anterodorsal aspect. The subcosta touches or almost touches vein 1 on part of the extent of the second costal cell, but has distinct and complete sclerotisation, and, though there is a distal divergence at the pterostigma, the intervening space is partly sclerotised. I am unable to demonstrate a significant degree of difference in my material of the centrioncine taxa in the separation of these two veins. Feijen's study is based on a much larger range of centrioncine taxa than is my present one, but, even with this reservation, it is apparent that neither of his two stated apomorphies can be logically treated as evidence for accepting a monophyletic group *Centrioncus* sensu Feijen. I therefore recommend that *Teloglabrus* Feijen be treated as a synonym of *Centrioncus* Speiser.

Shillito (1971) and Feijen (1989) refer to a median suture-like groove of the facial region of some diopsids as the facial sulcus. A comparison between various diopsid taxa, commencing with the less apomorphic *Centrioncus*, shows that the facial sulcus does not divide the face medially as has been assumed, but that the facial sulcus is actually the face, which has become greatly narrowed in more advanced diopsids (e.g., *Diopsis*, *Teleopsis*) by the encroachment of the more strongly sclerotised parafacial. The supposed absence of the sulcus in species of *Sphyracephala* and *Pseudodiopsis* (Feijen, 1989: p. 68) is due to smaller difference in degree of sclerotisation between parafacial and face and less narrowing of the face in these taxa (see Fig. 23). Differences in degree of development of the facial sulcus among the groups within the genus *Sphyracephala* may have been exaggerated. Among the diverse *Sphyracephala* material available to me, the specimen with the seemingly most distinct facial sulcus is one of *S. brevicornis* (Say) in which the face has collapsed slightly in drying. The distinction between face and parafacial in *Sphyracephala* is demonstrated by the presence of microtrichia on the crazed cuticle of the former (Fig. 24), compared with minute socket-based macrotrichia on the smooth cuticle of the latter (Fig. 23), though this is hard to appreciate without electron microscopy.

The so-called facial teeth of certain diopsids are lobes on the ventral margin of the genoparafacial sclerite, not of the face.

The Tanypezidae

Except in the classification of Griffiths (1972), the Tanypezidae have generally been referred to the superfamily Diopsoidea (or its equivalent under other names). The alternative association between Tanypezidae and "Heteromyzidae" proposed by Griffiths has been discarded (D. McAlpine, 1985) as based on convergent character states or on apomorphies which may date too far back in the phylogenetic history of the Schizophora to be classed as synapomorphies for this particular association. *Heteromyza* and allied genera almost certainly represent a particular development within the tribe Heleomyzini (sensu D. McAlpine) of the Heleomyzidae. Modern authors, following Hennig (1958), have generally considered that the genus *Strongylophthalmyia* forms a monophyletic group with the more typical tanypezids. Following Colless & D. McAlpine (1970) and Griffiths (1972), I prefer to include *Strongylophthalmyia* in the Tanypezidae, despite the obvious differences, because of their close agreement in many structures. Some differences between Tanypezidae and Strongylophthalmyiidae given by J. McAlpine (1989) apply for the separation of New

World forms, but not or less accurately for separation of some Old World species of *Strongylophthalmyia*, which are more morphologically diverse.

The Tanypezidae do not show clear morphological evidence of close relationships to any other family of Diopsoidea, though they provide a mixture of features of several of these families; e.g., the presence of a mesopleural bristle is shared only with Nothybidae, and the presence of a subcostal break in the costa and of divergent postvertical bristles agrees with the groundplan of the Psilidae. The presence of prothoracic precoxal bridges agrees with taxa of several diopsoid families, but the details of shape and contour of the prosternum, with its broad, ventrally exposed bridges, can be very like those of *Gobrya*, particularly in some *Strongylophthalmyia* species. However, as I can find no other significant points of resemblance between *Gobrya* and Tanypezidae, I interpret the resemblance as probably due to convergence.

The tanypezid *Neotanypeza dallasi* (Shannon) and several *Strongylophthalmyia* species have a well differentiated presutural bristle, and the former also has a posterior intra-alar ("inner postalar") and some well developed posteroventral bristles on the distal part of the fore femur. These look like the homologues of the bristles so named in certain taxa of Heleomyzoidea, Nerioidea, Tephritoidea, and other superfamilies, but such bristles do not occur in more typical diopsoid flies. (The true postalar bristle in the Diopsidae approximates in position to the intra-alar in other taxa. See autapomorphy (c) for that family).

The structure and relations of antennal segments 2 and 3 in Tanypezidae are much more like those of many taxa of Nerioidea than of any other Diopsoidea (except for the almost certainly derived condition in Diopsidae). The facial structure is unlike that of any other Diopsoidea and typical of the Nerioidea (e.g., certain Pseudopomyzidae, Neriidae, etc., see D. McAlpine, 1996). The strongly recurved anal crossvein (transverse section of CuA_2 or of CuA) is unlike that of any other diopsoid fly, but is similar to that of the pseudopomyzid genera *Heloclusia* and *Latheticomyia*, which I have regarded as somewhat primitive taxa of Nerioidea. However, no undoubted nerioid fly known to me has a prosternal structure remotely resembling that of Tanypezidae.

In *Strongylophthalmyia* spp. segment 7 of the female has the tergite and sternite fused by elimination of the pleural membrane, but the segment becomes desclerotised posteriorly. In *Tanypeza* (see Steyskal, 1987a: fig. 4) sclerotisation of segment 7 is represented by two pairs of longitudinal strips. Neither of the above conditions is typical of the Diopsoidea, but that of *Strongylophthalmyia* is not far from that of the Nerioidea, in which the tergite and sternite are fused to form an oviscape. The condition in *Tanypeza* may be derived either from that of *Strongylophthalmyia* or from a more plesiomorphic condition in which a separately sclerotised tergite and sternite have each been divided longitudinally.

While I do not claim to understand the relationships of the Tanypezidae to other taxa of Schizophora, were I to make an arbitrary superfamily assignment of the family on the basis of least improbability, this assignment should probably be to the Nerioidea.

The Somatiidae

The Somatiidae are a small probably very uniform family of flies, including only the genus *Somatia* restricted to the Neotropical Region. The species are listed by Steyskal (1970b). Steyskal (1958) made a case for their close relationship to the tephritoid family Richardiidae. J. McAlpine (1989) and Colless & D. McAlpine (1991) treated the Somatiidae as a family of Diopsoidea, and a relationship to the diopsoid family Psilidae has sometimes been accepted (e.g., by Hennig, 1971). Griffiths (1972), however, included *Somatia* in the Periscelididae, and rejected some further historical attempts at determining somatiid relationships. This diversity of opinion is indicative of the difficulty in deciding the systematic position of the Somatiidae within the Schizophora.

The antenna of Somatiidae has the essential features described above for the diopsoid families Syringogastridae and Psilidae. Taxa with these antennal features occur also in the superfamilies Tephritoidea, Asteioidea, Ephydroidea, and Muscoidea (= Calyptrata), as used in the classification of Colless & D. McAlpine (1991), so that further consideration of somatiid relationships will focus only on these superfamilies. The Somatiidae have none of the more distinctive features of Muscoidea so that relationships with this superfamily need not be further considered. The Ephydroidea (syn. Drosophiloidea) probably have as groundplan apomorphies distinct prothoracic precoxal bridges and symmetrical protandrial sclerites. In these features the Somatiidae are too plesiomorphic to have been derived from within the limits of the Ephydroidea, and wide divergence in other characters provides no grounds for suspecting any unusual homoplasy in these characters.

My study of comparative morphology indicates that, in the groundplan of the Schizophora, tergites 1 and 2 are imperfectly separated, that there is a linear transverse membranous zone between these tergites centrally, and a separate visible suture on each side running to the lateral margin where there is a notch or incision. This condition exists in at least some taxa of numerous schizophoran families. Also an oblique internal ridge on each side, running from the lateral suture towards the anterior margin of tergite 1, is present either in the groundplan of the Schizophora or of a substantial part thereof. In *Somatia* there is a long, sharply defined, impressed suture separating tergites 1 and 2 in the medial region, though the membranous line is indistinct; laterally the suture is obsolete, but there is a sclerotised oblique internal ridge on each side. From the relatively few taxa of the family Richardiidae at present available to me (representatives of subfamilies

Epiplateinae and Richardiinae) it appears that total absence of the suture between tergites 1 and 2 is probably a groundplan apomorphy for the family. Therefore *Somatia*, which retains a well marked suture, would not seem to belong within the Richardiidae.

The female postabdomen of *Somatia* (Steyskal, 1958: fig. 3) includes a definite free sternite behind segment 7, and the terminal parts are not fused into an aculeus. These conditions probably provide sufficient evidence for excluding *Somatia* from the superfamily Tephritoidea, to which the Richardiidae belong, even though some richardiids have apparently a (? secondarily) divided aculeus (Steyskal, 1987b). The presence of a large male tergite 6 (Steyskal, 1958; Griffiths, 1972) alone would negate any close relationship to the Richardiidae and allied tephritoid families. The very elongate distiphallus in the male and annular tergosternite 7 in the female of *Somatia* are conditions so frequently acquired in the Schizophora that they can no longer be considered to indicate an affinity with the Tephritoidea. The above considerations induce me to discard any hypothesis of close relationship between the Somatiidae and the tephritoid families.

Returning to a comparison of Somatiidae and the Diopsoidea, the unusually large, neck-like pronotum of *Somatia* is reminiscent of the Diopsidae and Syringogastridae, though detail of the articulation with the occipital part of the head is different. The deeply sclerotised metathoracic postcoxal bridge resembles that of Diopsidae, Syringogastridae, *Gobrya*, and some psilids, but such a postcoxal bridge has been derived many times in the Schizophora, e.g., several times in each of the families Platystomatidae and Tephritidae. It is particularly frequent in elongate flies with deep thorax and often wasp-like form, and is an element of the megamerinoid character set (D. McAlpine, 1997).

The glabrous arista (apart from its long, bipectinate rays) of the Somatiidae (see Fig. 7) contrasts with that of typical diopsoid taxa, which have pubescence on the basal part of segment 6, and on segments 4 and 5 when present. Among the typical diopsoids, only some of the more advanced diopsids show reduction (usually not complete absence) of this pubescence.

The apomorphic loss of the suture between abdominal tergites 1 and 2, apparently in the groundplan of the Diopsoidea, provides a difficulty for inclusion of Somatiidae in this superfamily, just as it does for its placement in the Richardiidae, as mentioned above. The Somatiidae also differ from all more typical diopsoids in the presence of strongly convergent postvertical bristles and a well differentiated cheek bristle (perhaps even to be identified as a vibrissa). The presence of a mesopleural bristle is shared with the Nothybidae and the doubtfully diopsoid family Tanypezidae, but not the Psilidae, the diopsoid family with which the Somatiidae have sometimes been closely associated.

Because the possible synapomorphies of Somatiidae and Diopsoinea are not very persuasive, and because of the above disagreements with the hypothetical groundplan of the Diopsoidea, I think that the hypothesis of close relationship between the Somatiidae and the Diopsoidea should be discarded.

Of the previously floated hypotheses on somatiid relationship, there remains only the question of affinity with the family Periscelididae. The Periscelididae are placed in the superfamily Asteioidea by Colless & D. McAlpine (1991) and in the suprafamily Asteioinea of the superfamily Opomyzoidea by J. McAlpine (1989). The former authors' Asteioidea and the latter's rather similar Asteioinea are not very strongly supported by cladistic evidence, and each should be regarded as a provisional grouping. There is lack of evidence that the diverse family-group taxa included in Opomyzoidea by J. McAlpine cohere in even a few of the postulated groundplan apomorphies (including three autapomorphies) listed by him. A critical analysis of this grouping is beyond the scope of this paper, but I know of no convincing evidence that these taxa of Opomyzoidea (sensu J. McAlpine) share a common ancestral state of, for instance, "face membranized along vertical midline," or "wing contrastingly patterned." Also, the fate of tergite 7 is unknown for these taxa (it is generally absent in likely outgroups to the Opomyzoidea), and, in the groundplan of some included families, sternite 7 is no more reduced and no more closely fused with sternite 8 than it is in likely outgroups. I therefore cannot recognise any validity in the broad superfamily Opomyzoidea of J. McAlpine, and I adhere provisionally to the separate superfamilies Asteioidea and Opomyzoidea of Colless & D. McAlpine.

Griffiths (1972) regarded the Periscelididae as consisting of the subfamily Periscelidinae (with approximately the same limits as used by Mathis, 1993) plus the genus *Somatia*. His case for monophyly of this family concept relies on five apomorphic conditions (by inference autapomorphies), numbered (1) to (5), which I review as follows:

(1) Anal vein (cu_{1b}+1a) abruptly cut off apically, not reaching margin.

This condition occurs in the groundplans of most families of Asteioidea, as well as Psilidae, Syringogastridae, Diopsinae, *Gobrya*, and a very large number of other schizophoran taxa.

(2a) Only one fronto-orbital bristle present.

This is the usual condition for Periscelidinae. The absence of such bristles in *Somatia* could have been achieved either by reduction of a single fronto-orbital or by simultaneous reduction of members of a series. We have no means of deciding which process was the relevant one, unless we first assume derivation from the periscelidine condition, adopting a circular argument.

(2b) ... ocellar bristles standing near ocellar prominence, not between ocelli.

This description seems to refer to the greater distance between the sockets of the ocellar bristles than that between the posterior ocelli. This condition applies to both Periscelidinae and *Somatia*, but is less marked in *Somatia* than in some species of Periscelidinae, in which subfamily there is some variability in the distance between the ocellars. I do not find this degree of

resemblance so distinctive, as compared with that in hypothetically related taxa that retain the ocellar pair of bristles, to convince one of synapomorphy. Most of the more diverse acalyptrate families in which ocellar bristles are commonly present show diversity in their placement, and this instability must often result in similarity which is not related to phylogenetic proximity.

(3) 7th abdominal tergum and sternum (female) fused, forming ring which includes the 7th pair of spiracles.

As mentioned above, this condition could be cited to support various relationship hypotheses for *Somatia*. Fusion of tergite 7 with sternite 7 has arisen many times in the Schizophora, and the superfamilies Nerioidea and Tephritoidea are the only major groups with the condition consistently present.

(4) Pregenital sclerite (male) extending ventrally on either side; 7th abdominal spiracles lying within this sclerite.

Actually, in *Somatia* the dorsal pregenital sclerite (apparently fused sternites 7 and 8) extends further downwards on the left side than on the right, because of inclusion of the laterally placed sternite 7. Such a condition is frequently found in the Schizophora as a stage in an often repeated reduction series (see D. McAlpine, 1985; 1988). In *Gobrya* and in numerous similarly reduced taxa the condition occurs with inclusion of one or more spiracles enclosed in the compound sclerite (Fig. 8).

(5) Aedeagus (male) slender and ribbon-like, supported by broad strip of flexible sclerotisation.

The "ribbon-like" or tubular aedeagus of the Periscelidinae is now known to show some diversity (e.g., Mathis, 1993; Mathis & Papp, 1992). As an elongate, flexible tubular or strap-like aedeagus occurs in many families of acalyptrate Schizophora (in addition to most tephritoid families), this is not a very particular point of resemblance between Periscelidinae and *Somatia*. Some groups containing species with flexible, strap-like aedeagus also include others with quite different aedeagal structure (e.g., Clusiidae, Teratomyzidae, the heleomyzid tribes Allophylopsini and Gephyromyzini).

I consider that, viewed in the broader field of schizophoran morphology, the supposed evidence for monophyly of the taxon Periscelidinae + *Somatia* does not hold up well.

In the broader concept of Periscelididae accepted by D. McAlpine (1983) and Mathis (1993) there is a distinctive apomorphy of the arista. Segment 5 (primitively the middle segment of the arista) is rather short, very asymmetrical, and reduced on the outer side, and the base of segment 6 is asymmetrically oblique. This structure can be traced through the periscelidid genera *Scutops, Periscelis, Cyamops*, and *Stenomicra*. In examined material of *Stenomicra*, segment 5 has disappeared, but the oblique base of segment 6 is retained. The aristal structure of *Somatia* (Fig. 7) does not fit into this sequence. Segment 5 is more elongate, ovoid, and almost symmetrical; segment 6 is not noticeably oblique at the base and lacks the general tendency seen in periscelidids (also in Nothybidae but not in Syringogastridae) for the dorsal rays to be crowded towards the base of the segment.

For these reasons I believe that the Somatiidae should not be merged with the Periscelididae. The Somatiidae have several strongly developed apomorphies, which have had a transforming effect on their general morphology, so that it is difficult to establish what the morphology of its lineage must have been before it reached such a degree of specialisation. I am unable at present to adduce a superfamily placement for this family.

The status of the Diopsoidea (Nothyboidea)

As deduced by Hennig (1958), there appears to be a morphologically coherent group of families, which may be termed the Diopsoidea, on the evidence of numerous cross-resemblances between the included families. Included taxa are the Psilidae, Nothybidae, Syringogastridae, Diopsidae, and *Gobrya*, but this coherence does not extend to the Megamerinidae, Tanypezidae, and Somatiidae, as indicated above and by D. McAlpine (1997).

J. McAlpine (1989) gave a list of seven groundplan autapomorphies for the Diopsoidea. I reject this set of character states as conditions that are too widely distributed through major schizophoran taxa to have any value as indicators of particular relationships among the Diopsoidea. Thus, they do not posses the attributes of primal autapomorphies discussed above. I note that the whole set occurs also in the families Pallopteridae, Lauxaniidae, Anthomyzidae, and Drosophilidae, *inter alias*, except that the fate of sternite 7 in the two latter is sometimes unclear (as it is in many diopsoid taxa).

Though the most certain morphological basis for monophyletic taxa is a set of rigorously tested autapomorphies (except where there is a fossil record of extraordinary completeness), I contend that this is an ideal scenario that may be frequently unattainable (D. McAlpine, 1996). It is therefore possible that a group of families may be or may approximate to a monophyletic group without providing clearly indicated groundplan autapomorphies. I suggest that the superfamily Diopsoidea is possibly such a group. It is also a useful category for classifying the component families and data concerning them, especially as strong evidence for relating any of them to families placed outside the Diopsoidea has not been discovered. Two of its component families (Psilidae and Diopsidae) are represented unambiguously in Baltic amber (Hennig, 1965), which is mainly of Upper Eocene origin. The superfamily, if really monophyletic, must therefore have originated very early in the Tertiary, i.e. very early in the history of the Schizophora. Also the comparative morphology of the diopsoid families seems to confirm that the Diopsoidea are a fairly "basal" group of Schizophora, i.e. their earliest members possessed an overall relatively primitive morphology, despite the later acquisition of striking apomorphies among the derived taxa.

The following is a list of groundplan conditions (a–r) for the hypothetical clade Diopsoidea, derived from my study of the included taxa. As they are generally not demonstrable autapomorphies, they do not prove the monophyly of the superfamily. They can have some value as diagnostic characters in so far as included taxa should have a morphology derivable from this character set, rather than in complete agreement with it.

(a) *Body and legs elongate.* This condition is not to be precisely defined, but is more noticeable in the diopsoid families than in most representatives of such other superfamilies as Sciomyzoidea, Ephydroidea etc. Its use as a primal synapomorphy for uniting the Nerioidea and Diopsoidea (J. McAlpine, 1989) cannot be accepted because the elongate habitus has arisen many times in various schizophoran groups, and because it is not well developed in the nerioid groundplan.

(b) *Differentiated frontal triangle (ocellar plate) present.* This is probably a plesiomorphy shared with several other schizophoran superfamilies.

(c) *Face sclerotised.* This is a probable plesiomorphy, and contrasts with the condition in the nerioid groundplan, where the face is desclerotised on its lower median part (D. McAlpine, 1996).

(d) *Vibrissa absent.* Hennig (1958) regarded the presence of a vibrissa as an apomorphy relative to the groundplan of the Schizophora. However, its status may vary in different schizophoran taxa, and present lack of understanding of outgroups for the Diopsoidea makes its status indeterminate.

(e) *Differentiated series of postocular setulae or bristles absent.* In certain representatives of all schizophoran superfamilies recognised by Colless & D. McAlpine (1991), except the highly autapomorphic Brauloidea, there is a linear series of postocular setulae differentiated from other hairs or setulae on the postocular surface of the head. These tend to lose their identity in certain taxa when there is general reduction of cephalic macrotrichia, or when this region becomes covered with long, dense hairs or mollisetae from which the postocular setulae are not differentiated. The taxonomic distribution of uniseriate postocular setulae suggests that their presence is in the groundplan of the Schizophora. I have failed to find a series of postocular setulae in any taxon here referred to the Diopsoidea (after removal of the Tanypezidae and Somatiidae), so that its loss may be a groundplan condition of this superfamily, if it is monophyletic. (*Psila rosae* [Fabricius] has one or two distinct bristles behind each outer vertical bristle, but these are not members of a particular series, and are absent in other available psilids.) The frequency of arisal of loss of the postocular series in the Schizophora, including its loss or reduction in certain taxa of Nerioidea, which have paralleled the morphological tendencies of the Diopsoidea in a number of ways, leads me to doubt its value as an indicator of monophyly for the Diopsoidea.

(f) *Antennal segments 2 and 3 with psilid-like structure, including the following elements: segment 2 has a distodorsal longitudinal slit, and deeply concave terminal surface; segment 3 is variably elongate, deflexed at an angle to the axis of the two basal segments, and has a dorsobasal prolongation that fits into the cavity of segment 2; the arista is attached dorsobasally on segment 3.* Presence of the structure in outgroups, as discussed above, virtually precludes its interpretation as an autapomorphy for Diopsoidea. The psilid-like antenna occurs in all families here retained in the Diopsoidea except the Diopsidae, where its loss is evidently an autapomorphy from comparison with other diopsoid families, particularly the sister group Syringogastridae.

(g) *Anterior notopleural bristle reduced.* All taxa of Diopsoidea known to me are without the anterior notopleural bristle, except for some species of *Gobrya*, which have a small but well differentiated bristle.

(h) *Presutural bristle (sometimes termed "posthumeral") absent.* This is a consistent condition in the Diopsoidea, but Feijen (1989) misidentifies the posterior notopleural of diopsids as a "presutural bristle".

(i) *Posterior intra-alar bristle (or "inner postalar") absent.* This is a consistent condition in the Diopsoidea.

(j) *Sternopleural bristle absent.* This is a consistent condition in the Diopsoidea, and contrasts with the groundplan condition of Nerioidea (D. McAlpine, 1996).

(k) *Fore femur without series of elongate posteroventral bristles.* In the superfamilies Sciomyzoidea, Heleomyzoidea, Opomyzoidea, Asteioidea, Ephydroidea, Tephritoidea, and Muscoidea (sensibus Colless & D. McAlpine, 1991), also in the primitive nerioid family Pseudopomyzidae, there is commonly a series of long, strong posteroventral bristles on the fore femur. The nearest approach to this condition in Diopsoidea occurs in some Diopsinae, where their degree of development together with outgroup comparison does not convince me of their homology with similarly placed bristles in the above-mentioned superfamilies.

(l) *Preapical dorsal tibial bristle absent.* A single well differentiated preapical dorsal bristle is commonly present on all or some tibiae in the superfamilies Sciomyzoidea, Heleomyzoidea, Ephydroidea, Muscoidea, and much less frequently in the Opomyzoidea. The Diopsoidea are one of the schizophoran superfamilies in which the preapical dorsal bristle is uniformly absent.

(m) *Fore basitarsus without male-restricted terminal ventral process* (see D. McAlpine, 1991: fig. 42; 1996). I have inferred that this process is probably present in the groundplans of the Sciomyzoidea, Heleomyzoidea, and Nerioidea, but I know of no instances of its presence in any other schizophoran superfamily, including the Diopsoidea.

(n) *Second basal and anal cells relatively long, but latter not markedly produced posterodistally.* This condition is a little variable in the superfamily and its range may well include the groundplan condition for the Schizophora. It contrasts with that of numerous families in other superfamilies.

(o) *Vein 7 (2A or A_2) absent without trace beyond alular region.* This condition, consistent within the Diopsoidea, is of fairly frequent arisal in the Schizophora. J. McAlpine (1989) gives it as a synapomorphy for

Diopsoidea and Nerioidea, but the presence of vein 7 in representatives of two subfamilies of the nerioid family Micropezidae negates this interpretation.

(p) *Abdominal tergites 1 and 2 fused, with total loss of intervening suture.* This character is discussed above in connection with the Somatiidae.

(q) *Male tergite 6 relatively large.* This condition may be a plesiomorphy, but distinguishes most taxa of Diopsoidea from many other schizophoran taxa in which tergite 6 is markedly reduced or absent in the male.

(r) *Female abdominal segment 7 with separately sclerotised tergite and sternite.* This plesiomorphic condition contrasts with that of the groundplans of the superfamilies Nerioidea and Tephritoidea.

Relationships of *Gobrya*

The megamerinid hypothesis

Hendel (1913), in including *Syrittomyia* and *Gobrya* in the Megamerininae, defined the latter group on a number of superficial characters, particularly on several of those that I have listed (D. McAlpine, 1997) as the "megamerinoid character set". All seven elements of this set can be identified to some extent in *Gobrya*, as follows: (1) the body form is very elongate; (2) bristling on the thorax is greatly reduced, though some species have both pairs of notopleurals; (3) the base of the wing is much narrowed; (4) the metapleuron and metasternum together form a prominence for insertion of the hind coxae; (5) the metathorax has a deep postcoxal bridge; (6) the hind femur is ventrally spinose and somewhat larger than other femora; (7) the abdomen has a narrow, hinge-like junction with the thorax. Evidence has been provided (D. McAlpine, 1997) that this whole set of apomorphies is subject to simultaneous convergence in numbers of phylogenetically remote taxa, and cannot be relied upon in deducing monophyly.

Hennig (1958) indicated a set of five groundplan apomorphies for Megamerinidae s.l. These included four particular bristle losses, one of them considered doubtful, and the thickened, spinose condition of the hind femur. Of these, loss of the ocellar bristle is not present in some taxa he included in Megamerinidae s.l., and the thickening of the hind femur of *Gobrya* is not nearly as marked as in some other taxa sharing the megamerinoid character set.

Recently (D. McAlpine, 1997) I reviewed a set of characters occurring in Megamerinidae s.str. which suggest relationship to the superfamily Nerioidea. None of these nerioid-like conditions occurs in *Gobrya*. To be specific, *Gobrya* differs from true megamerinids in having a completely sclerotised face, simple, quite short ptilinal fissure, simple antennal socket, reduced and virtually concealed frontal lunule, nothybid- or psilid-like antenna, very extensively sclerotised prosternal region with precoxal bridge, and relatively short female postabdomen. Also the hypandrium and aedeagus of *Gobrya* is of such completely different structure from that of true megamerinids that none of the distinctive component parts present in the latter can be homologised with any part in *Gobrya*. The one notable feature they have in common, loss of the aedeagal apodeme, does not, therefore, provide a plausible synapomorphy.

I conclude that *Gobrya*, like several other genera of diverse relationships, shows remarkable morphological convergence with the Megamerinidae, but shares no likely synapomorphies with the latter. In view of the numerous significant differences, it is improbable that they are referable to the same superfamily.

The syringogastrid hypothesis

Colless & D. McAlpine (1975) suggested that *Gobrya* "may be related" to the Syringogastridae, and Ferrar (1987) mentioned *Gobrya* under that family without further discussion. As shown above, I consider that the Diopsidae represent the sister group of the Syringogastridae (these two families constituting the prefamily Diopsoinea), but *Gobrya* does not share their distinctive set of synapomorphies (Table 1). This comparison demonstrates that the closest conceivable relationship between *Gobrya* and Syringogastridae would be a sister group relationship between *Gobrya* on one hand and the Diopsoinea on the other, but it does not in itself provide support for such a relationship.

Evidence for relationship between *Gobrya* and Syringogastridae-Diopsidae is difficult to substantiate. The loss of the postvertical and dorsocentral bristles is perhaps such evidence, but loss of the former is shared with Nothybidae, and, in view of the loss of the supra-alar and usual reduction of the postalar bristle also in *Gobrya*, absence of the dorsocentral therein could be interpreted as part of an independent process of general bristle reduction on this region of the thorax. Acquisition of the megamerinoid character set (or most of its elements) is another apomorphy common to both groups, though not necessarily a valid synapomorphy.

Gobrya differs from the Syringogastridae in having the following attributes: ptilinal fissure shortened; parafacial suture obsolete; facial cuticle smooth; upper occiput concave; subcranial region small; antennal segment 2 with recessed terminal surface facing forwards (instead of downwards); arista unsegmented (three-segmented in Syringogastridae, see Figs 16, 18), its series of dorsal rays extending almost to base; precoxal bridge of prothorax very broad, its surface largely facing ventrally; fore coxa not much longer than hind coxa; subcosta complete, distally meeting costa; spiracle of abdominal segment 1 in pleural membrane (not in tergite).

I conclude that evidence for close relationship between *Gobrya* and Syringogastridae-Diopsidae is weak and ambiguous.

The nothybid hypothesis

D. McAlpine (1982) placed *Gobrya* tentatively in the Nothybidae. There are several interesting points of similarity between *Gobrya* and *Nothybus*.

There is remarkably detailed similarity between *Gobrya* and *Nothybus* in antennal structure. In addition to the generally psilid-like features present in the possible groundplan of the Diopsoidea, the arista (strictly antennal segment 6) is bipectinate, with the series of dorsal rays (but not the ventral series) extending almost to its base. The rather similar antenna of the Psilidae and Syringogastridae differs in having the pedicel more cap-like, with terminal articular surface facing ventrally, and no long dorsal rays of segment 6 arising near base of the latter. However, the above conditions of the antenna in *Gobrya* and *Nothybus* exist also in the Periscelididae, and, with a little variation, in Neurochaetidae, Drosophilidae, and other families. In *Nothybus* segment 6 is much more thickened basally than in *Gobrya*, and segments 4 and 5 are well sclerotised but quite short and annular. The latter condition could be an approach towards loss of segments 4 and 5 as in *Gobrya*. For these reasons, I cannot feel certain that the antennal structure of *Gobrya* and *Nothybus* includes synapomorphies.

The facial region of both *Gobrya* and *Nothybus* is well sclerotised and convex, but the contour and proportions are so different in the two genera that it is doubtful if any synapomorphy can be inferred. Again, both genera have the upper occiput concave, but the disagreement in contour of the vertex and arrangement of the bristles of this region renders any synapomorphy uncertain.

Gobrya and *Nothybus* have a large prosternal plate bordered laterally by unusually broad precoxal bridges with extensive ventral exposure. Though there seems a possibility of synapomorphy here, there is a little difference in detail. The posterior part of the sternal plate is raised and medially grooved in *Gobrya*, but almost flat in *Nothybus*. The precoxal bridge of *Nothybus* is even broader than that of *Gobrya*.

Both genera have the ptilinal fissure shortened, without descending lateral arms (Fig. 15). Though there is some variation in the ptilinal fissure among families referred to the Diopsoidea, I can find no other examples where it is as reduced as in *Gobrya* and *Nothybus*. The condition could therefore be a synapomorphy.

Gobrya differs from *Nothybus*, notably, but not exclusively, in having the following morphological conditions: head very broadly depressed; all frontal bristles absent except those at vertex; face and cheek region with extensive ventrally facing surface; ocelli located near vertex; arista unsegmented; prothoracic spiracle vertically elongate; posterior notopleural callus absent; scutellum and subscutellum short; pleurotergite without setulae; the following thoracic bristles much reduced or absent: supra-alar, postalar, dorsocentral, lateral scutellar, anepisternal; metathorax and base of abdomen as in megamerinoid character set; femora not attenuated, with variably developed ventral spines; tarsi not longer than their respective tibiae; wing with only one (anterodorsal) costagial bristle; male postabdomen strongly asymmetrical in almost all parts; male tergite 6 fused with sternite 8; distiphallus not strap-like; female with fused, annular tergite 6 and sternite 6.

I conclude that, while *Gobrya* and *Nothybus* share several apomorphies (possible synapomorphies), the morphological difference between them is very substantial. Apart from the possible connection between Nothybidae and Psilidae, these differences do not, however, seem to indicate synapomorphies of either genus with any other taxon. While it is conceivable that *Gobrya* and *Nothybus* may be sister groups, any such relationship must be due to a very ancient common ancestry, for which much evidence has been obscured by subsequent morphological change.

Some plesiomorphies of *Gobrya*

In *Gobrya* there is a well differentiated oblique katepimeral sclerite (barette) between the posteroventral margin of the pteropleuron and the anterodorsal part (meron or meropleurite) of the hypopleuron, but separated from the latter by a sharply defined, tympanum-like membranous panel along its entire length (Fig. 28). This panel I designate the katepimeral membrane. Apart from *Gobrya*, no taxon here referred to the Diopsoidea possesses a katepimeral membrane, but it shows a varying degree of development in several other schizophoran superfamilies, including Conopoidea, Sciomyzoidea, Heleomyzoidea, Nerioidea, Tephritoidea, and Muscoidea. It is particularly well developed in the Tanypezidae, and narrow but defined in the Somatiidae. I have not detected it in any representative of Aschiza.

This character distribution suggests that the katepimeral membrane may have been acquired early in the evolution of the Schizophora, perhaps even in the stem-group, but has become reduced or lost in many lineages. On this basis the well defined katepisternal membrane in *Gobrya* is probably a plesiomorphy. The absence of the membrane in the other families of Diopsoidea would therefore be an apomorphy, but because the monophyly of the Diopsoidea is uncertain, and because there is variation of development of the membrane in those superfamilies in which it has been detected, this condition may not be a groundplan condition of the superfamily, even supposing that *Gobrya* does not belong here.

At least two undetermined *Gobrya* species (West Malaysia, Australian Museum) have a well-differentiated anterior notopleural bristle. In the other available species (including *G. cyanea* [Enderlein]) there is only the usual posterior notopleural bristle, the anterior one being undifferentiated from the few fine hairs of the region (the 0+1 condition). The 1+1 condition of the notopleural bristles occurs in the groundplans of probably all superfamilies of Schizophora, with the possible exception noted below, and it is probable that this is a homologous condition preserved in the groundplan of *Gobrya*. However, as far as I can ascertain, no other taxon here

considered to belong in the Diopsoidea possesses an anterior notopleural bristle, the 0+1 condition being usual. The consistency of this apomorphic condition in the Diopsoidea would suggest it to be an autapomorphy for the superfamily, but for the difficulty imposed by the apparently plesiomorphic condition in *Gobrya*. Exclusion of *Gobrya* from the Diopsoidea would seem to smooth out this difficulty. On the other hand, reduction of the anterior notopleural is an element of the frequently acquired megamerinoid character set (D. McAlpine, 1997), and, as the various component taxa of Diopsoidea have a strong tendency towards the kind of habitus associated with this character set, convergence in the 0+1 notopleural condition is not deemed highly improbable. Hence exclusion of *Gobrya* from the Diopsoidea on the above grounds seems not to be justified.

While the presence in *Gobrya* of these two plesiomorphies, otherwise uniformly replaced by their corresponding apomorphies in diopsoid taxa, is not regarded as disproof of its postulated diopsoid affinities, it emphasises the distinctness of *Gobrya* from other diopsoid taxa.

Groundplan autapomorphies of *Gobrya* (AA), contrasted with plesiomorphic states in other diopsoid families (P)

These are selected as apomorphies not present in the groundplans of the two most plausible outgroups, Nothybidae and Syringogastridae + Diopsidae. Even if these are not the nearest outgroups, and the relationships of *Gobrya* lie elsewhere in the Schizophora, these character states remain as very probable autapomorphies.

(a) *Head not broader than high (P)/ head broadly depressed (AA).*

(b) *One or two fronto-orbital bristles present (P)/ fronto-orbital bristles absent (AA).*

(c) *Parafacial suture distinct (P)/ parafacial suture obsolete (AA).*

(d) *Arista 3-segmented (P)/ arista unsegmented (AA).*

(e) *Postalar bristle (on summit of postalar callus) present (P)/ postalar bristle absent (AA).*

(f) *Abdominal tergite 1 completely sclerotised anteriorly (P)/ abdominal tergite 1 with deep membranous sinuation in anterior margin (AA).*

(g) *Male abdominal tergite 6 separately sclerotised (P)/ male abdominal tergite 6 fused with sternite 8 (AA).*

(h) *Epandrium and surstyli approximately symmetrical (P)/ epandrium and surstyli very asymmetrical (AA).*

(i) *Aedeagus not fused with hypandrium, at least its basal part approximately symmetrical (P)/ aedeagus rigidly fused with hypandrium, very asymmetrical (AA).*

(j) *Aedeagal apodeme present (P)/ aedeagal apodeme absent (AA).*

(k) *Female abdominal segment 6 with separate tergite and sternite (P)/ female abdominal segment 6 with tergite and sternite fused into a complete annulus (AA).*

Taxonomic conclusions

Taking into consideration degrees of difference between acalyptrate families in general, the evidence for wide phylogenetic isolation of *Gobrya* from other taxa, and the likelihood of future stability in classification, I consider that the most appropriate course is to place *Gobrya* in a separate monogeneric family. The Gobryidae n.fam. are well supported as a monophyletic group by eleven identified autapomorphies and a low degree of morphological diversity among the included species. The family may be placed in the provisional superfamily Diopsoidea, and, if there is particular (sister-group) relationship to a single diopsoid family, this may be to the Nothybidae, though the evidence for this is ambiguous.

Because of the apparently low morphological diversity and incomplete taxonomic knowledge of the only included genus, a cladistic treatment of the family is not warranted at present.

Gobryidae n.fam.

Type genus: *Gobrya* Walker

Diagnostic description. Fully winged, moderately small, elongate flies, with reduced chaetotaxy and somewhat braconid-like habitus. Head large, somewhat depressed, much broader than thorax; postfrons oblong, its surface entirely occupied by a uniformly sclerotised plate apparently derived from ocellar plate or triangle, with fine setulae at orbital margins; frontal lunule largely concealed; ptilinal fissure short, its descending lateral arms undeveloped; facial region broad, uniformly sclerotised, convex in profile, its lower part extensively facing ventrally; parafacial suture obsolete; upper occiput concave; supracervical region with compact, convex setulose callosity; eye large, much broader than postfrons in dorsal view; ocelli well developed, posterior ones on ridge of vertex; inner and outer vertical bristles present, the former much, the latter slightly behind ridge of vertex; other cephalic bristles absent; membranous subcranial region small, broadly oval. Antenna: segment 1 short; segment 2 short, deeply slit dorsally, with distal surface facing forwards; segment 3 elongate, deflexed at angle to rest of antenna, with dorsobasal process inserted into cavity of segment 2; arista unsegmented, probably through desclerotisation of segments 4 and 5, so that segment 6 appears to arise from a gibbosity on segment 3 a little beyond basal process of latter; segment 6 irregularly bipectinate, with dorsal rays more numerous than ventral ones densely pubescent on basal part. Prelabrum (postclypeus) short and deep; palpus and proboscis moderately developed; labella well developed, reflexed.

Thorax elongate, without neck-like anterior extension; pronotum very short; prosternal region with large basisternal plate, raised and medially grooved posteriorly, with very broad, largely ventrally facing precoxal bridges anteriorly; scutellum short; subscutellum distinct, convex,

but not very prominent; prothoracic spiracle vertically elongate; narrow oblique sclerite (remnant of katepimeron) sharply demarcated from upper part of meron (meropleurite) by a well defined membranous strip; metathorax forming a prominent base for hind coxae, not cylindrically produced at attachment of abdomen (in contrast to Syringogastridae and Diopsidae); postcoxal bridge deep, but deeply sinuate on dorsal side; apical scutellar, posterior notopleural (not on callosity), and sometimes anterior notopleural bristles present; postalar bristle either undifferentiated or small but distinct, located on angle of postalar callus and not dorsomedially displaced (i.e. located as in Syringogastridae, not as in Diopsidae); scutellar bristle inserted on very slight tubercle; other thoracic bristles absent or scarcely differentiated from setulae. Legs of moderate proportions, but markedly increasing in length in the order fore, mid, hind; fore coxa slightly longer than hind coxa, inserted far from anterior end of thorax (but less far than in Nothybidae); hind femur with thickened, spinescent seriate anteroventral and posteroventral bristles; other femora often with less developed ventral spinescent bristles; mid tibia with large apical ventral spur; tibiae otherwise without bristles; fore and mid tarsi much more slender than hind one; basitarsi cylindrical, without series of short cuneate setulae (in contrast to Syringogastridae and Diopsidae). Wing narrow, attenuated basally; tegula very small; anterodorsal costagial bristle usually present but weak; costa extending to vein 4, without break or visible weakening at either humeral or subcostal position, with numerous fine setulae, but no stouter spines or spinules; subcosta complete, well sclerotised, terminating well before end of vein 1 so as to leave a clear subtriangular area of subcostal cell between the two veins; second basal, discal, and anal cells all elongate and complete; distal section of vein 6 well sclerotised but rather short, sometimes reaching approximately to wing margin; vein 7 indistinguishable beyond alular incision; alula much reduced, with incomplete marginal fringe; squama (lower calypter) quite undeveloped.

Abdomen very slender, with anterior segments forming a slender petiole which is more pronounced in male; abdomen dorsoventrally compressed at its hinge-like articulation with thorax; tergite 1 and sternite 1 with deep membranous sinuation in anterior margin (as component of hinge mechanism, in contrast to that of Syringogastridae and Diopsidae); tergites 1 and 2 quite fused; other preabdominal tergites well separated by intersegmental membrane (in contrast to Syringogastridae); sternites 1 to 5 all separate and well sclerotised; spiracles of segments 1 to 5 all located in pleural membrane, that of segment 1 well removed from margin of tergite.

Male postabdomen. Protandrium with single asymmetrical sclerite, apparently consisting of fused tergite 6 and sternites 6, 7, and 8, enclosing two pairs of spiracles (6 and 7). Epandrium large, asymmetrically subspherical; surstyli separated from margin of epandrium by membrane, very asymmetrical and of unequal size; a separate, undivided, plate-like subepandrial sclerite present between bases of surstyli; hypandrium desclerotised; aedeagus short and broad, with very complex, irregular, asymmetrical sclerotization; aedeagal apodeme absent; ejaculatory sclerite rather small, slender, bent near middle; cerci well developed, separate but attached to sides of proctiger, only slightly asymmetrical.

Female postabdomen short, not markedly extensile. Segment 6 large, with tergite and sternite fused into a complete ring (its form suggesting that it consists very largely of tergite), enclosing spiracle laterally; segment 7 shorter, with separate tergite and sternite and spiracle enclosed in tergite; cerci separate, very broad; spermathecae 3, with pigmented cuticular lining to vesicles (at least in *G. cyanea*).

Key to families which have been associated with the Diopsoidea

1. Antennal segment 2 without narrow dorsal slit in distal margin; segment 3 not deflexed at an angle to basal segments, usually not much longer than deep 2

—— Antennal segment 2 with narrow dorsal slit in distal margin; segment 3 deflexed at an angle to basal segments, usually markedly longer than deep 4

2. Scutellum with pair of setiferous horns; fore leg generally raptorial with enlarged coxa and incrassate femur; second basal and discal cells confluent ..... Diopsidae

—— Scutellum without setiferous horns; fore leg not thus modified; second basal and discal cells separated 3

3. Mesopleural bristle absent; costa not broken or incised at end of subcosta; prothoracic precoxal bridge absent; hind femur incrassate, ventrally spinose ..... Megamerinidae

—— Mesopleural bristle present; costa broken or incised at end of subcosta or its distal vestige; prothoracic precoxal bridge well developed; hind femur neither incrassate nor spinose ..... Tanypezidae

4. Pronotum enlarged and prominent, holding head away from mesothorax 5

—— Pronotum very short, so that head can be held close to mesothorax 6

5. Convergent postvertical bristles present; arista glabrous basally; hind femur neither incrassate nor spinose; abdomen broadly oval; abdominal tergites 1 and 2 partly separated by an impressed suture ..... Somatiidae

—— Postvertical bristles absent; arista pubescent basally; hind femur incrassate and ventrally spinose; abdomen slender; tergites 1 and 2 fused, without visible suture ..... Syringogastridae

6. Ptilinal fissure well developed, with descending lateral arms; prothoracic precoxal bridge absent; postvertical bristles usually present, divergent ..... Psilidae

—— Ptilinal fissure short, without descending lateral arms; prothoracic precoxal bridge broad; postvertical bristles absent 7

7. Fronto-orbital bristles large; arista 3-segmented; hind femur not thicker than mid femur; metathorax without postcoxal bridge ..... Nothybidae

—— Fronto-orbital bristles absent; arista unsegmented; hind femur thicker than mid femur; metathorax with deep postcoxal bridge ..... Gobryidae

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Table 1. Synapomorphies for Syringogastridae and Diopsidae compared with character states of *Gobrya*.

Syringogastridae + Diopsidae	***Gobrya***
Inner vertical bristle vestigial (though outer vertical retained)	Inner vertical bristle present
Pronotum well developed, projecting well beyond margin of mesoscutum in dorsal view	Pronotum undeveloped (as in most schizophorans)
Supra-alar carina strongly developed	Supra-alar carina absent
Metathorax produced into a short posterior cylinder, articulating with abdominal segment 1; tergite 1 ensheathing cylinder when abdomen is raised	Metathorax not cylindrically produced, tergite 1 with deeply sinuate, non-ensheathing anterior margin
Tarsal sawline present at least on posterior side of mid basitarsus	Tarsi without sawlines
Intersegmental membrane between abdominal tergites 2 and 3 reduced	Intersegmental membrane between tergites 2 and 3 normally developed, enabling overlap of tergites and articulation between segments

Table 2. Classification of taxa of Diptera-Eremoneura mentioned in text.

SERIES (GRADE) ASCHIZA

Superfamily Platypezoidea (Phoroidea)*
- ?Opetiidae
- ?Lonchopteridae
- Platypezidae
- Ironomyiidae
- Sciadoceridae
- Phoridae

Superfamily Syrphoidea
- Syrphidae

SERIES SCHIZOPHORA

Superfamily Diopsoidea (Nothyboidea)*
- Ungrouped
  - Psilidae
    - *Loxocera* Meigen
    - *Psila* Meigen
  - Nothybidae
    - *Nothybus* Rondani
  - Gobryidae
    - *Gobrya* Walker (*Syrittomyia* Hendel)*
- Diopsoinea
  - Syringogastridae
    - *Syringogaster* Cresson
  - Diopsidae
    - Centrioncinae
      - *Centrioncus* Speiser (*Teloglabrus* Feijen)*
    - Diopsinae (Sphyracephalinae)*
      - *Prosphyracephala* Hennig
      - *Sphyracephala* Say
      - *Pseudodiopsis* Hendel
      - *Diopsina* Curran
      - *Diasemopsis* Rondani
      - *Cyrtodiopsis* Frey
      - *Teleopsis* Rondani
      - *Diopsis* Linné

Superfamily Sciomyzoidea
- Coelopidae
  - *Coelopa* Meigen

Superfamily Heleomyzoidea
- Heleomyzidae (Heteromyzidae)*
  - Heleomyzini
    - *Heteromyza* Fallén
  - Rhinotorini
    - *Rhinotora* Schiner

Superfamily Nerioidea
- Pseudopomyzidae
  - *Heloclusia* Malloch
  - *Latheticomyia* Wheeler
- Micropezidae
- Megamerinidae

Superfamily Chloropoidea
- Chloropidae
  - *Aragara* Walker

Superfamily Tephritoidea
- Platystomatidae
  - Angitulinae
    - *Giraffomyia* Sharp
- Richardiidae

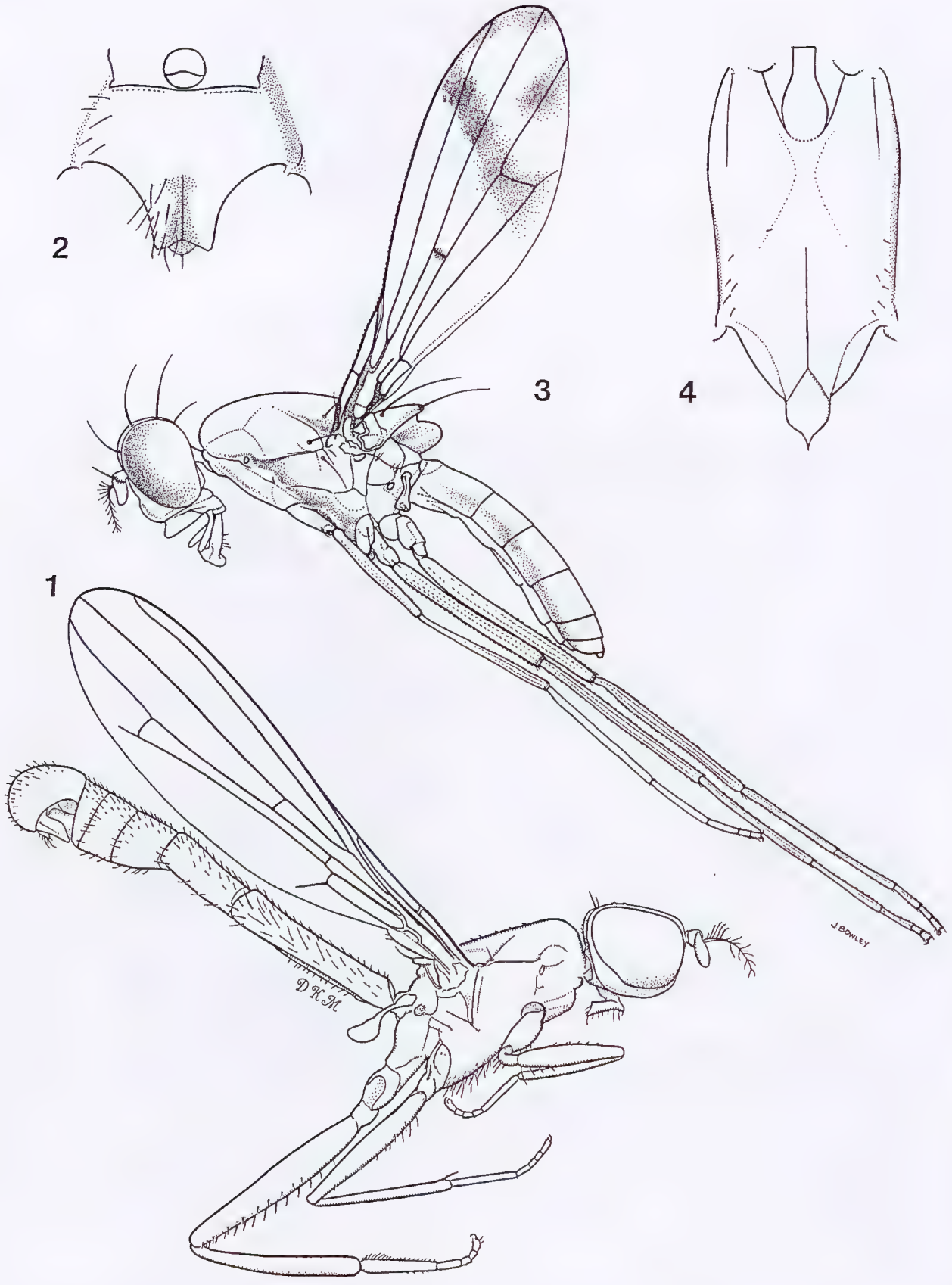
Superfamily Asteioidea
- Periscelididae
  - Periscelidinae
    - *Scutops* Coquillett
    - *Periscelis* Loew
  - Stenomicrinae
    - *Stenomicra* Coquillett
  - Unplaced
    - *Cyamops* Melander
- Neurochaetidae
  - *Anthoclusia* Hennig
  - *Neurocytta* D. McAlpine
  - *Neurotexis* D. McAlpine
  - *Neurochaeta* D. McAlpine
- Teratomyzidae

Superfamily Ephydroidea
- Drosophilidae
  - *Drosophila* Fallén
- Curtonotidae
  - *Axinota* Wulp
  - *Cyrtona* Séguy
  - *Curtonotum* Macquart
- Diastatidae
- Ephydridae
  - *Ochthera* Latreille
  - *Stratiothyrea* de Meijere
- Cryptochetidae

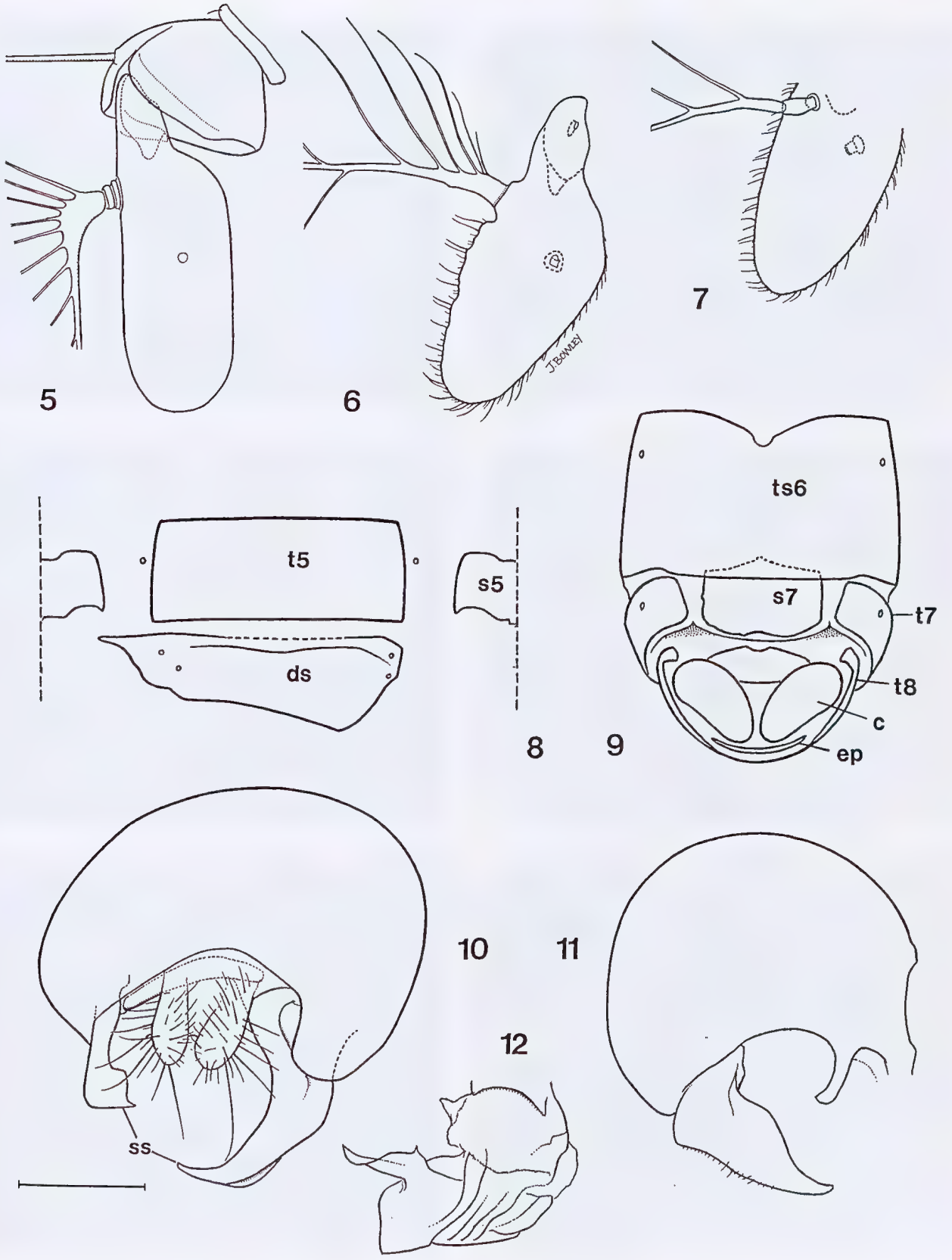
Superfamily Muscoidea (Calyptratae)*
- Glossinidae

Superfamily Uncertain
- Tanypezidae (Strongylophthalmyiidae)*
  - *Tanypeza* Fallén
  - *Neotanypeza* Hendel
  - *Strongylophthalmyia* Heller
- Somatiidae
  - *Somatia* Schiner

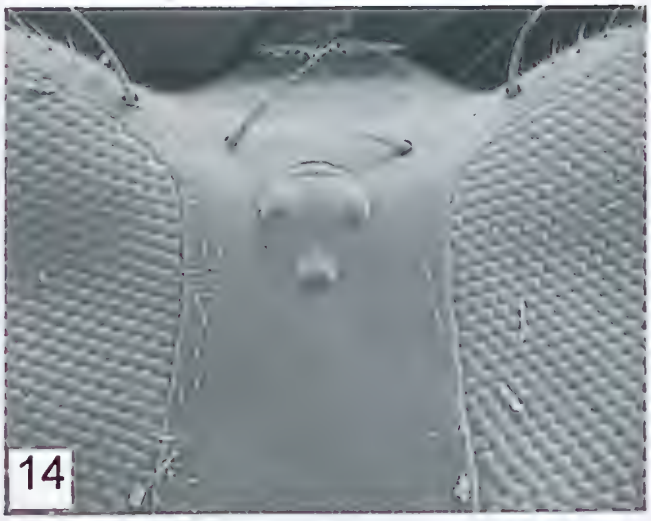
* Names in brackets are treated as synonyms.

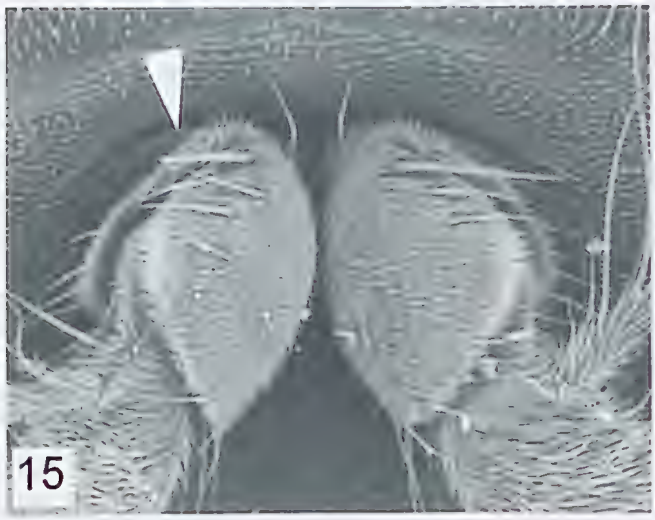


Figs 1–4. 1, *Gobrya cyanea* (Enderlein), adult male. 2, *G. cyanea*, prosternum. 3, *Nothybus decorus* de Meijere, adult female. 4, *N. decorus*, prosternum.

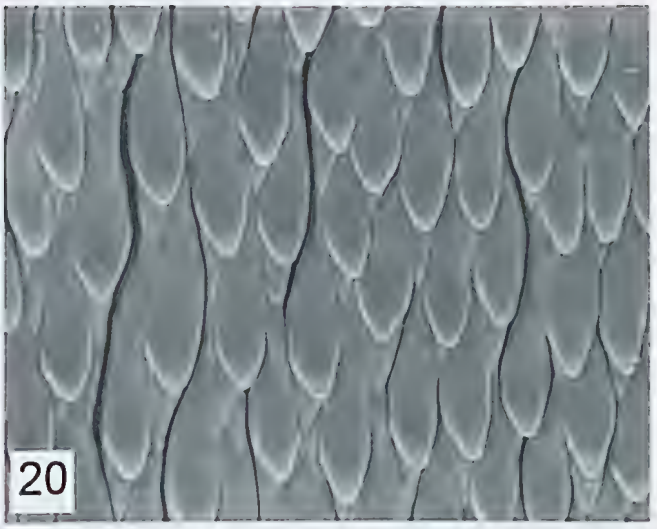


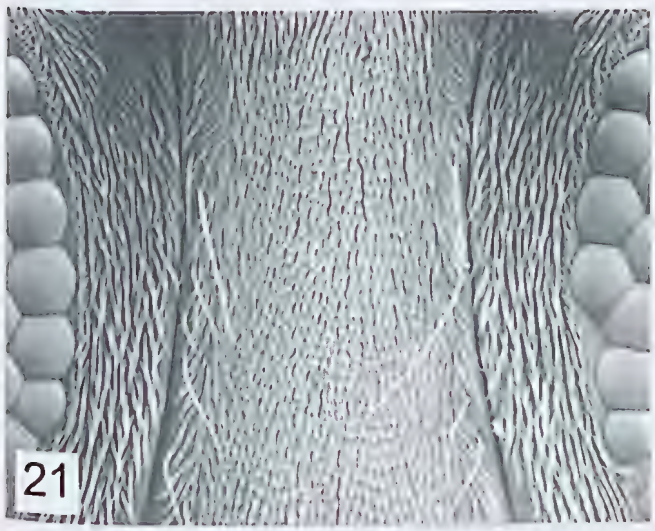
Figs 5–12. 5, *Nothybus decorus*, left antenna, vestiture and arista (segment 6) simplified. 6, *Gobrya cyanea*, antennal segments 3–6 (note absence of segments 4, 5). 7, *Somatia aestiva* (Fabricius), antennal segments 3–6. 8, *G. cyanea*, protandrogram (sclerites of segments 5–8 of male abdomen shown as if split along median ventral line and spread flat). 9, *G. cyanea*, female postabdomen, ventral view. 10, 11, *G. cyanea*, epandrium and associated structures, posterior and right lateral views. 12, *G. cyanea*, aedeagus, right lateral view. c, cercus. ds, compound dorsal sclerite probably including tergite 6 and sternites 6 to 8. ep, epiproct. s5–s7, sternites 5–7. ss, surstyli. t5–t8, tergites 5 to 8. ts6, tergosternite 6.

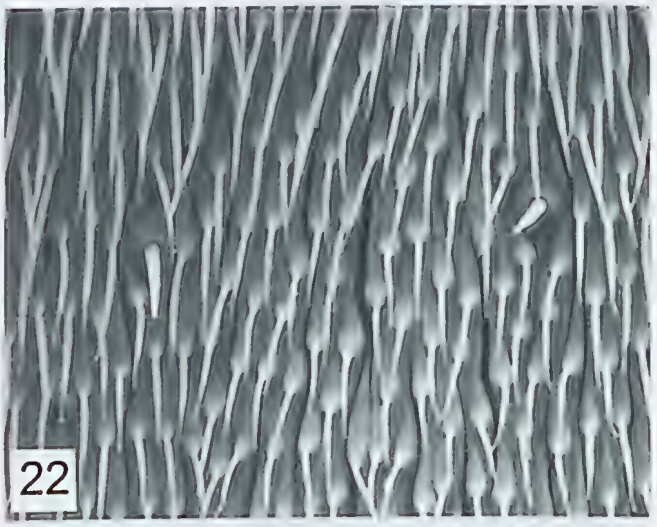


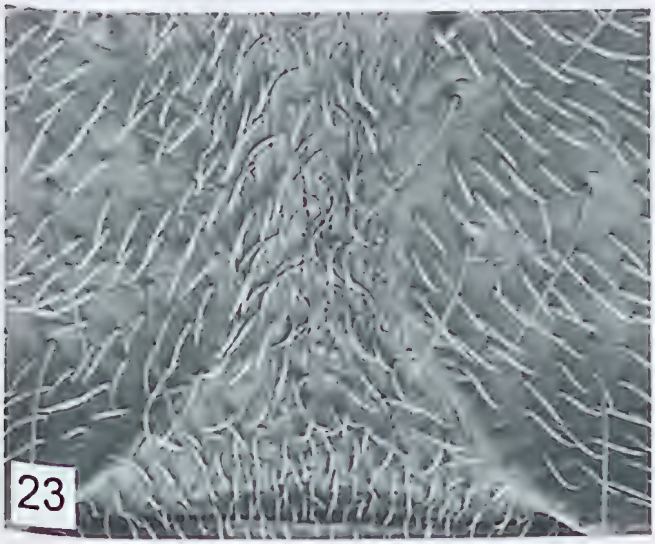


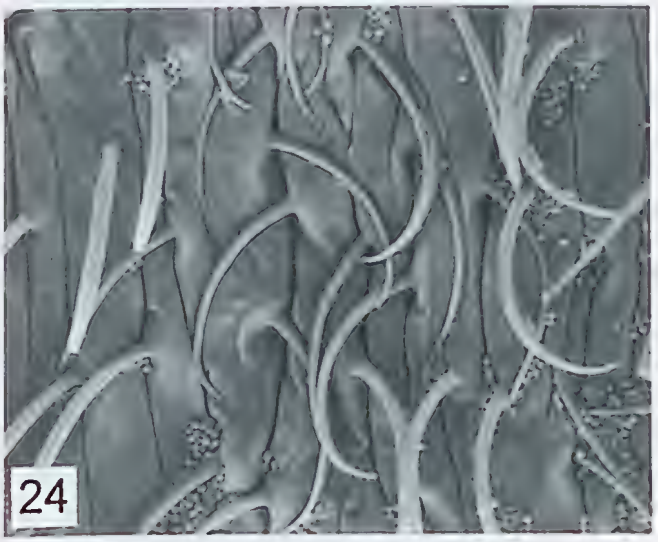
Figs 13–18. 13, *Gobrya cyanea*, head, facial view ×50. 14, *G. cyanea*, vertical region of head ×105. 15, *G. cyanea*, region of antennal bases ×249, ptilinal fissure indicated. 16, *G. cyanea*, base of arista ×800, showing direct insertion of segment 6 into socket of segment 3. 17, *Syringogaster* sp. (Costa Rica), facial region of head and antennae ×144. 18, the same base of left arista ×1990, segments 4, 5 indicated.



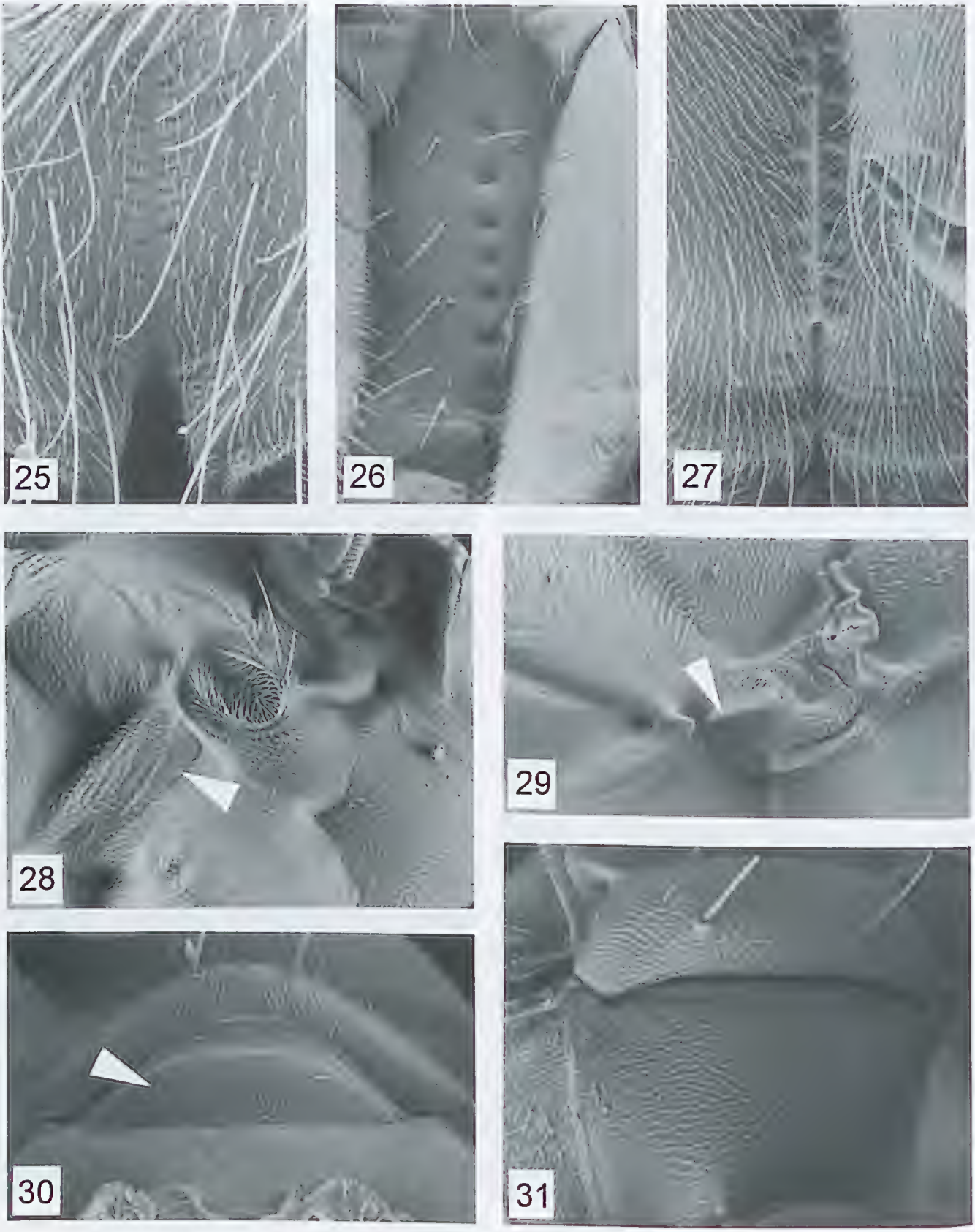




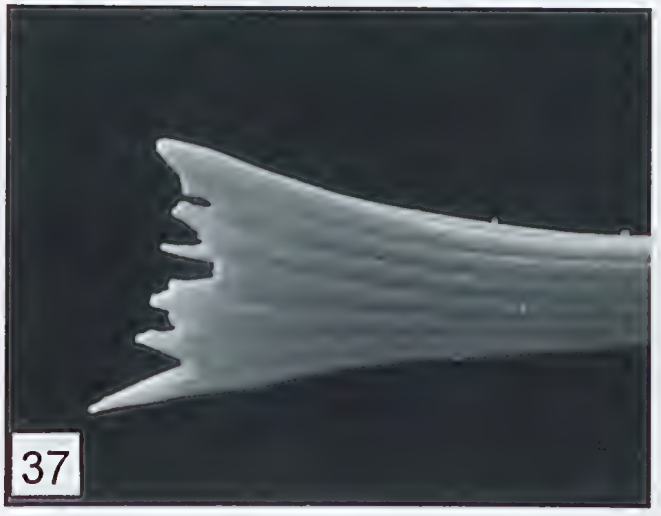




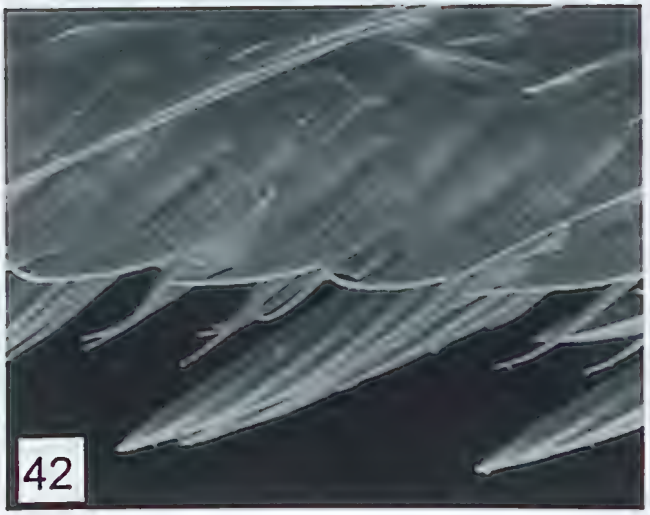
Figs 19–24. 19, *Syringogaster* sp. (Costa Rica), lower facial region ×138, scaly central section indicated. 20, *Syringogaster papaveroi* Prado, scaly crazed cuticle of face ×2350. 21, *Centrioncus decoronotus* Feijen, mid facial region ×231. 22, *C. decoronotus*, detail of central section of face ×1075, showing microtrichose crazed cuticle and a pair of macrotrichia. 23, *Sphyracephala beccarii* Rondani, lower part of face and parafacials ×436. 24, *S. beccarii*, microtrichose crazed cuticle of face ×2140.



Figs 25–31. 25, *Gobrya cyanea*, median ventral region of sternopleura ×358, showing rugosity (? incipient sternopleural pits). 26, *Syringogaster* sp. (Costa Rica), median ventral region of sternopleura ×185, showing single median series of pits. 27, *Sphyracephala beccarii*, median ventral region of sternopleura ×235, showing double series of pits. 28, *G. cyanea*, part of left side of thorax ×165, showing metathoracic spiracle, katepimeral membrane indicated. 29, *Syringogaster papaveroi*, same part of thorax ×162, haltere removed, cuticular spine indicated. 30, *G. cyanea*, scutellum and postscutellar structures ×149, subscutellum indicated. 31, *Syringogaster* sp. (Costa Rica), same parts ×127, subscutellum obsolete.



Figs 32–37. 32, *Syringogaster* sp. (Costa Rica), anterior part of thorax and occiput ×100, humeral lamella indicated (absent in *S. papaveroi*). 33, *Cyrtodiopsis* sp. (W. Malaysia), smae parts ×62. 34, *Syringogaster* sp. (Costa Rica), left supra-alar region of thorax ×234, supra-alar carina indicated, postalar bristle at right. 35, *Centrioncus decoronotus*, same parts ×138, supra-alar carina (with supra-alar bristle) indicated, postalar bristle at upper right. 36, *Cyrtodiopsis* sp., same parts ×117, supra-alar carina indicated, bristles not differentiated from modified hair-like macrotrichia. 37, *Cyrtodiopsis* sp., apex of modified macrotrichium of mesoscutum ×2810.



Figs 38–43. 38, *Syringogaster papaveroi*, metathoracic region, right lateral view ×75, abdomen and haltere removed, secondarily enlarged metanotum indicated. 39, *Cyrtodiopsis* sp., metathoracic region and base of abdomen ×79, abdominal tergite 1 (indicated) concealing metanotum. 40, *Syringogaster* sp. (Costa Rica), mid tarsus, anterior view ×221, sawline indicated. 41, the same, detail of sawline on mid basitarsus ×2250. 42, *Centrioncus decoronotus*, part of posterior sawline of mid basitarsus ×1740. 43, *Cyrtodiopsis* sp., the same ×1485.

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Icasma Collin and an Allied New Genus *Glyphidopeza,* from New Zealand (Diptera: Empidoidea; Ceratomerinae)

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ABSTRACT. The endemic New Zealand genus *Icasma* Collin (Diptera: Empidoidea; Ceratomerinae) is reviewed and includes the following seven species: *I. aequabilis* Plant, *I. setosa* n.sp., *I. fascipennis* n.sp., *I. longicauda* n.sp., *I. masneri* n.sp., *I. singularis* Collin (lectotype designated), *I. tararua* n.sp. An allied new genus, *Glyphidopeza* is described from New Zealand and includes the following new species: *G. fluviatilis, G. longicornis*. A key to species and illustrations of male and female terminalia are provided. *Icasma* is divided into two species-groups and the phylogenetic relationships of the species are analysed.

SINCLAIR, BRADLEY J., 1997. *Icasma* Collin and an allied new genus *Glyphidopeza,* from New Zealand (Diptera: Empidoidea; Ceratomerinae). Records of the Australian Museum 49(2): 195–211.

The subfamily Ceratomerinae (Diptera: Empidoidea) is confined to southern South America (including high altitude Equador), eastern Australia, New Zealand, and Norfolk Island (Sinclair unpubl. data). It is a distinctive empidoid subfamily, recognised by its narrow wings and a small conus extending from the pedicel on which the first flagellomere is attached.

Three genera of Ceratomerinae are known from New Zealand. *Ceratomerus* Philippi as currently defined is a trans-Antarctic genus with 13 described (Plant, 1991) and at least 20 undescribed species from New Zealand. This is nearly double the number of species that are known from Australia (Sinclair unpubl. data). The second genus, *Icasma* Collin, is endemic to New Zealand and may be divided into two informal species-groups on the basis of the male cercus. The *I. singularis* Collin species-group includes six species (*I. aequabilis* Plant, *I. singularis* Collin, *I. setosa* n.sp., *I. fascipennis* n.sp., *I. longicauda* n.sp., *I. tararua* n.sp.) and the *I. masneri* group is monotypic. The third genus, *Glyphidopeza* n.gen., comprising two new species was collected from small cascading mountain streams on South Island. The wing venation is very primitive and possibly represents the sister group to the remaining ceratomerines. In this paper the latter two endemic New Zealand genera are described and illustrated.

Materials and methods

This study is based on more than 300 adult specimens borrowed from or deposited in the following institutions: Australian Museum, Sydney (AMS); The Natural History Museum, London, England (BMNH); Canadian National Collection of Insects, Ottawa, Canada (CNC); New Zealand Arthropod Collection, Auckland, New Zealand (NZAC). Abbreviations given here are used throughout the text to indicate deposition of specimens. All type material of Plant (1990), which was originally stored in ethanol, have been critical-point-dried, mounted, and relabelled.

Terms used for adult structures primarily follow those of J. McAlpine (1981), except male terminalia where terms of Cumming *et al.* (1995) and Sinclair (1996) are used. Terms for the female terminalia follows Sinclair (1995). The term "bristle" is used for differentiated large setae on the head, mesonotum, and legs bearing a particular name or one of a series with a particular name, e.g., notopleural bristle, dorsocentral bristle, ocellar bristle. The hair-like setae located between facets of the compound eye are referred to as ommatrichia *sensu* D. McAlpine (1991).

Label data of holotypes are cited in full, with original spellings, punctuation and dates; lines are delimited by a slash, and a semicolon separates data quoted from different labels. Paratypes and additional material are listed under area codes, which refer to specific regions of New Zealand (Crosby *et al.*, 1976): AK—Auckland, BR—Buller, FD—Fiordland, HB—Hawke's Bay, MB—Marlborough, NC—North Canterbury, NN—Nelson, RI—Rangitikei, SD—Marlborough Sounds, TK—Taranaki, WD—Westland, WN—Wellington, WO—Waikato. Scanning electron micrographs were produced on a Cambridge Stereoscan 120.

Specimens were collected by sweep net, yellow pans, and malaise traps. Yellow pans were distributed along streams, creeks, and wet depressions.

Key to genera of New Zealand Ceratomerinae

1. Cell cu*p* present; cell dm long and narrow, distally emitting 3 veins ..... *Glyphidopeza* n.gen.

—— Cell cu*p* absent; cell dm generally short, distally emitting 2 veins 2

2. R_{4+5} branched; Sc complete; wing long and narrow, lacking dark band; stigma present or absent; first flagellomere long, slender and tapering ..... *Ceratomerus*

—— R_{4+5} unbranched; Sc incomplete; wing broad and short, often with dark band; stigma absent; first flagellomere acutely ovate ..... *Icasma*

Glyphidopeza n.gen.

Type species. *Glyphidopeza fluviatilis* n.sp.

Recognition. In addition to the characters listed in the key, *Glyphidopeza* is distinguished from all other ceratomerine genera by the stout ocellar bristle inserted anterolaterally to the anterior ocellus, posteriorly positioned proboscis, presence of pseudotracheae, and the modified basitarsis of the male midleg.

Description. Male. *Head* (Fig. 26): eye with ommatrichia or bare; ocellar bristle inserted anterolaterally to anterior ocellus; 1 pair of postocellar bristles; 3 vertical bristles; postocular margin with row of long setae extending over half width of eye. Conus inserted into first flagellomere. Proboscis arising near back of head; palpus cylindrical; stipes one-third length of lacinia; lacinia fused to labial paraphysis; setae of labellum simple; pseudotracheae present (Figs 3,4).

Thorax: pruinescent patterns lacking; antepronotum narrow; acrostichal setae extending to prescutellar depression, uniserial except for erect anterior pair; 6–7 dorsocentral bristle, anterior pair forward and laterally displaced from line; 2 presutural supra-alars; 2 strong notopleurals; 2 postsutural supra-alars; 1 postalar; 2 pairs scutellar bristles. Antepronotum with 1 pair of short, widely spaced setae; laterotergite bare. Halter knob dark.

Wing: slender, infuscate; 1 long basicostal bristle; C circumambient, anterior margin of C with evenly spaced, spine-like erect setae; stigma absent; Sc complete; R_1 short, reaching costa well before mid-length of wing; R_{2+3} ending beyond radial fork; R_{4+5} branched or unbranched; cell bm small, faintly outlined; cell dm long, narrow and truncate, distally emitting 3 veins; cell cu*p* very narrow, pigmented; A_1 absent.

Legs: fore coxa less than twice length of mid or hind coxae. Fore and hind tibiae with posteroapical comb. First tarsomere of midleg with ventral notch, bearing modified setae. First tarsomere of foreleg longer than following 3 tarsomeres; tarsi somewhat flattened; fifth tarsomere broad, with median, dorsoapical protuberance; empodium pulvilliform.

Abdomen: concolorous with thorax, ventrum slightly paler. Tergite 7 complete, only partially desclerotized medially.

Female. Legs unmodified. Apical abdominal segments retracted into segment 7; apical margins of segment 7 not folded inwards; tergite 7 lacking posterior fringe of setae. Dorsomedial region of tergite 8 desclerotized; transverse fringe of short setae present; anterior margin with heavily sclerotized narrow, median plate, extending into segment 7. Tergite 10 (Fig. 5) undivided medially, bearing 3 pairs of spine-like setae; lateral margin with row of spine-like setae. Cercus membranous, retracted beneath tergite 10, bearing 3 setae. Genital fork small, slender; spermathecal receptacle large, oval, somewhat flattened, with short neck.

Biology. Both species of *Glyphidopeza* were either swept or collected in yellow pans from emergent rocks in cascading mountain streams.

Etymology. The generic name is derived from the Greek *glyphidos* (notch) and *peza* (foot), in reference to the modified first tarsomere of the male midleg. Its gender is feminine.

Key to species of *Glyphidopeza*

1. R_{4+5} branched; anterior postpronotal bristle subequal in thickness to posterior postpronotal bristle ..... *G. fluviatilis*

—— R_{4+5} unbranched; anterior postpronotal bristle much more slender than posterior postpronotal bristle ..... *G. longicornis*

Glyphidopeza fluviatilis n.sp.

Figs 3,4,5–7, 26–28, 34

Type material. HOLOTYPE male, "NEW ZEALAND MB/ Mt. Richmond For. Pk./ Butcher's Flat, 5.ii.1995/ B.J. Sinclair/ cascading creek"; "HOLOTYPE/ Glyphidopeza/ fluviatilis/ Sinclair [red label]" (NZAC). PARATYPES: **BR**—1 male, 8 females, Nelson Lakes NP, Lk. Rotoiti, Black Valley Str., 15–16.ii.1995; yellow pans, B.J. Sinclair (CNC,NZAC); 1 male, 5 females, Nelson Lakes NP, Lk. Rotoroa, Braeburn Tr., *Nothofagus* for., 7.ii.1995, B.J. Sinclair (NZAC); **MB**—20 males, 32 females, same data as holotype (AMS, CNC, NZAC); **NN**—2 females, Graham R. South Branch, Graham Valley, 17–18.ii.1995, yellow pans, B.J. Sinclair (CNC); 1 female, NW Nelson For. Pk., Oparara R., 8.ii.1995, B.J. Sinclair (NZAC).

Recognition. Males are distinguished from *G. longicornis* by the short first antennal segment (less than half the length of the first flagellomere) and a branched R_{4+5}.

Description. Wing length 1.5–1.6 mm.

Male. *Head* (Fig. 26): spherical, eyes bare and widely separated; face brown. Ocellar bristle long, divergent; 1 pair of short postocellar bristles, half length of ocellars; outer vertical bristle long, stout and lateroclinate over eye, longer than ocellar bristle; 2 inner vertical bristles. Antenna (Fig. 27) short, concolorous with head; scape less than half length of first flagellomere, with several long dorsal and ventral setae; pedicel with fringe of long setae; first flagellomere broadly triangular, clothed in long pruinescence; two-segmented arista short, first segment half as long as second; second segment of arista bearing long apical seta. Palpus half length of proboscis.

Thorax: brown, pleura slightly paler, acrostichal row more darkly pigmented. All bristles dark, stout; 6 dorsocentrals, 1 short anterior and 1 long posterior postpronotal bristles.

Wing (Fig. 34): C lacking long setae near base; R_{4+5} branched.

Legs: coxae and basal half of femora pale, remaining leg segments increasingly darkened. First tarsomere of midleg with ventral notch, bearing several flattened setae (Fig. 28). Mid femur with 2 long posterodorsal, apical bristles. Hind tibia lacking preapical dorsal bristle.

Terminalia (Figs 6,7): lateral lobes flanking phallus inconspicuous. Hypandrium lacking flap-like process; apex expanded about phallus; gonocoxal apodeme absent. Ejaculatory apodeme slender, fused to base of phallus. Epandrium lacking dorsal bridge; narrow, with long setae. Surstylus tapering to a narrow apex, bearing 1 long seta on posterior margin; distinctly articulated with epandrium at base; bacilliform sclerite broad, half width of epandrium. Cercus undivided, with several long setae surrounding anus.

Female. Similar to male except as follows: apex of labellum with cluster of more than 6 pairs of stout setae (Fig. 4). Legs unmodified. Terminalia as described under generic description.

Geographic distribution and seasonal occurrence. This species is known from northern South Island, collected in late summer.

Biology. Numerous specimens were collected in cascading streams associated with *Nothofagus* forests.

Etymology. The species name is derived from the Latin *fluviatilis* (of a stream) in reference to the habitat of this species.

Glyphidopeza longicornis n.sp.

Figs 1,2

Type material. HOLOTYPE male, "NEW ZEALAND MB/ Mt. Richmond For. Pk./ Butcher's Flat, 5.ii.1995/ B.J. Sinclair/ cascading creek"; "HOLOTYPE/ Glyphidopeza/ longicornis/ Sinclair [red label]" (NZAC).

Recognition. Males are distinguished from *G. fluviatilis* by a greatly lengthened first antennal segment (subequal in length to first flagellomere) and an unbranched R_{4+5}.

Description. Wing length 2.0 mm.

Male. *Head* (Fig. 1): dark, anterior margin flattened; eyes with ommatrichia and widely separated; face brown. Ocellar bristle short, stout, parallel; 1 pair of postocellar bristles, longer than ocellars; vertical bristles short, stout, subequal in length. Antenna long, paler than head; scape subequal in length to first flagellomere, with 2 long dorsal and 2 long ventral setae; pedicel oval with fringe of long setae; first flagellomere gradually tapering to slender apex, clothed in long pruinescence; two-segmented arista slightly shorter than first flagellomere; both segments subequal in length, second segment of arista lacking apical seta. Palpus two-thirds length of proboscis.

Thorax: dark brown, pleura slightly paler, scutum evenly pigmented. All bristles dark, stout; 7 dorsocentrals; 1 short, fine anterior and 1 long posterior postpronotal bristles.

Wing: basal third of C with several long setae; R_{4+5} unbranched.

Legs: coxae, femora and tibiae pale brown, tarsi dark brown. First tarsomere of midleg projecting obliquely with pair of sickle-shaped setae and several setulae (Fig. 2). Mid femur with 1 long dorsal, preapical bristle. Hind tibia with 1 preapical dorsal bristle.

Terminalia (not dissected): Cercus undivided, posteroapical margin of cercus with erect setae. Epandrium with darkly pigmented dorsoapical surstylus; surstylus broad.

Female. Unknown.

Geographic distribution and seasonal occurrence. This species is known from a single male collected together with *G. fluviatilis*.

Biology. This species was swept from a cascade in a small tributary of Doom Creek across from Butchers Flat campground. The creek emerged from a cool forest, dominated by *Nothofagus*.

Etymology. The species name is an adjective derived from the Latin *longus* (long) and *cornu* (horn), in reference to the long first antennal segment.

Icasma Collin

Icasma Collin, 1928: 22. Type species *I. singularis* Collin (original designation).

Recognition. This genus is distinguished from other ceratomerines by the acutely ovate first flagellomere, unbranched R_{4+5}, and the heavily sclerotized male cercus.

Description. Male. *Head* (Fig. 29): Eyes bare, nearly touching beneath antennae; face with white pruinescence; ocellar bristle long, divergent, inserted anteriorly to lateral ocelli; postocellar bristle divergent; 2 pairs of vertical bristles; postocular margin usually with short setae. Scape shorter than first flagellomere, with fine dorsal setulae and long, ventroapical seta, twice length of pedicel; fringe of setae on pedicel with long dorsal and ventral setae; first flagellomere acutely ovate with apical pruinescence (Fig. 30); two-segmented arista with short pruinescence. Proboscis (Figs 8,9) equal to height of head arising from anterior margin to middle of head; base of labrum lacking dorsal process; palpus short, oval, somewhat flattened, with several long, pale setae; lacinia pale, clearly separated from labium, half length of labium, apical quarter with frayed edges; stipes darkly pigmented, half length of lacinia; setae of labellum slender; pseudotracheae absent.

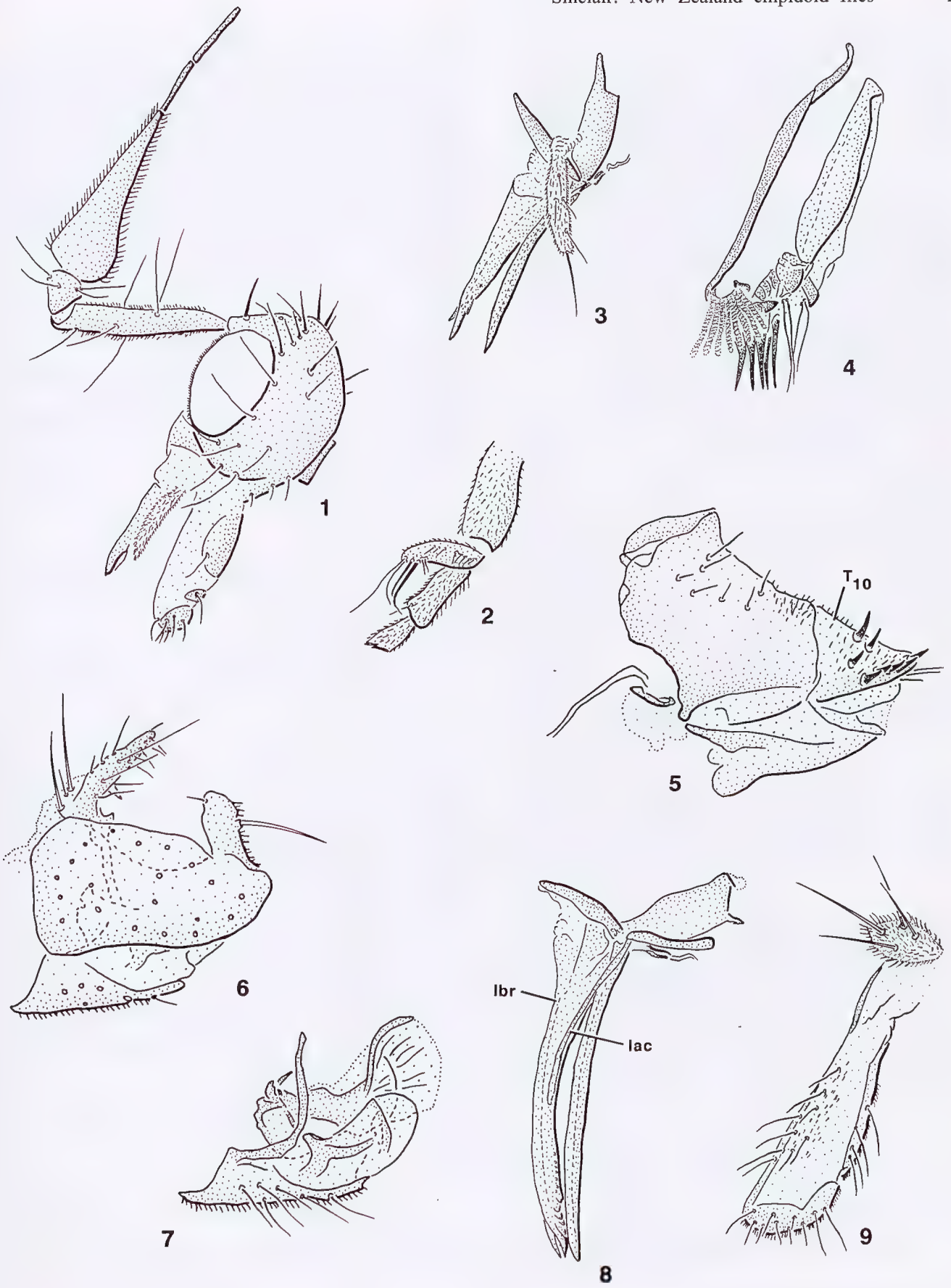
Thorax: vestiture reduced to discrete bristles; mesonotum often clothed in pruinescence. Acrostichals short, biserial or uniserial, with alternate setae divergent; 4 dorsocentrals; 1 postpronotal; 1 presutural supra-alar; 2 notopleurals, lower weak; 0–1 postsutural supra-alar; 1 postalar; 2 pairs scutellar bristles. Antepronotum with 1 pair of short setae; laterotergite bare. Halter knob variable in colour.

Wing: short and broad or long and slender, often with broad transverse band; stigma absent; 1 long basicostal bristle; C circumambient, although faint along posterior margin; C lacking erect setae; Sc incomplete; R_1 short, joining costa at basal third; R_{2+3} extending from middle to two-thirds length of wing; R_{4+5} unbranched; cell dm rectangular, distally emitting 2 veins; medial fork broad; cell cu*p* absent.

Legs: slender, lacking modified setae and processes; setae short, slender; hind tibia with conspicuous posteroapical comb. Tarsomeres unmodified, first tarsomere of foreleg shorter than following 3 tarsomeres; fifth tarsomere flattened dorsoventrally, apex straight, lacking apical lobe; empodium setiform with plumose apex.

Abdomen: faintly dusted with pruinescence; scattered short pale setae; terminalia shiny. Central region of tergite 7 membranous.

Male terminalia: hypandrium often with apical lobe(s); postgonite partially fused to phallus (Figs 10,17,20); gonocoxal apodeme short, slender. Ejaculatory apodeme



Figs 1–9. **1**, *Glyphidopeza longicornis*, head. **2**, *G. longicornis*, first tarsomere, male midleg. **3**, *G. fluviatilis*, female, labrum, hypopharynx. **4**, *G. fluviatilis*, female, labium (outer labellum removed). **5**, *G. fluviatilis*, female terminalia. **6**, *G. fluviatilis*, male terminalia. **7**, *G. fluviatilis*, hypandrium and phallus. **8**, *I. setosa*, labrum and hypopharynx. **9**, *I. setosa*, labium. Abbreviations: lac, lacinia; lbr, labrum; T, tergite.

slender, fused to base of phallus, not articulated. Epandrial halves separated, lacking slender dorsal bridge. Surstylus long and slender, projecting well beyond epandrium; lacking basal articulation; bacilliform sclerite broad, one-third width of epandrium. Cercus heavily sclerotized, bearing modified setae (Figs 11,12,15).

Female. Similar to male except as follows: generally larger in size, especially abdomen; wing occasionally with distinctive markings compared to male. Apical abdominal segments retracted into segment 7; apical margins of segment 7 not folded inwards; tergite 7 lacking posterior fringe of setae. Centre region of tergite 8 with deep U-shaped desclerotized zone; transverse fringe of long setae present; anterior margin lacking median plate. Anterodorsal margin of sternite 8 reduced to long, slender sclerite. Tergite 10 divided medially into rectangular sclerites; posterior margin with row of spine-like setae (Fig. 14); cercus with cluster of spine-like setae, similar to tergite 10. Slender, folded genital fork membranously connected to broad, sclerotized infolding of sternite 8; spermathecal receptacle large, spherical; base of spermathecal duct pigmented for more than diameter of receptacle.

Biology. Adults of *Icasma* were collected in forests close to streams, and swept from low vegetation in upland forests. *Icasma setosa* was collected near cool sphagnum filled pools in a darkly shaded *Nothofagus* forest. Although the immature stages are unknown, they probably inhabit cool, damp or moist soils.

Remarks. There is a single, undescribed female species from Chile (CNC) with R_{4+5} unbranched, but it is not considered congeneric on the basis of the following combination of characters: R_{2+3} extending to near wing tip; apical half of first flagellomere long and tapering; stigma present (yet faint).

Key to species of *Icasma*

1. Mesonotum with pruinescence confined to scutellum (Fig. 32) 2

—— Mesonotum either dusted entirely with pruinescence or with a median stripe (Figs 31,33) 5

2. Wing with broad, dark band (Figs 36,37) 3

—— Wing infuscate, lacking broad band (Figs 35,39) 4

3. Hindleg yellow, lacking dark band; surstylus long, slender and strongly arched, expanded apically bearing setulae (Fig. 20) ..... *I. singularis*

—— Hind femur and tibia with dark central band; surstylus short, expanding apically, bearing stout apical setae (Fig. 17) ..... *I. setosa*

4. First flagellomere brown, 1.5× longer than wide; arista shorter than antenna; surstylus short, broadly expanded apically (Fig. 10) ..... *I. aequabilis*

—— First flagellomere white, slightly longer than wide; arista longer than antenna; surstylus gradually tapering to broad apex (Fig. 16) ..... *I. longicauda*

5. Mesonotum entirely dusted with pruinescence (Fig. 33) ..... *I. tararua*

—— Mesonotum mostly shiny dark brown, with a median pruinescent stripe (Fig. 31) 6

6. Wing infuscate (Fig. 41); cercus with round apex (Fig. 23), posterior margin with subapical peg-like seta (*I. masneri* group) ..... *I. masneri*

—— Wing with wide, dark band (Fig. 36); cercus with narrow apex (Fig. 12), anterior margin with large, spine-like seta ..... *I. fascipennis*

The *Icasma singularis* group

This species group is characterised by short, broad wings, vein R_{2+3} short, extending to middle or just beyond middle of wing, and thickly sclerotized male cerci which are fused medially, bearing a pair of long, spine-like setae. The *singularis* group includes the following species: *I. aequabilis, I. fascipennis, I. longicauda, I. setosa, I. singularis*, and *I. tararua*.

Icasma aequabilis Plant

Figs 10,11, 35, 43

Icasma aequabilis Plant, 1990: 16.

Type material. HOLOTYPE male, NEW ZEALAND (WO)./ N.Is. Mt.Karioi.Raglan./ Malaise Trap by Wainui Str./ 12.x.85–20.x.1985./ coll. H.A. Oliver (NZAC). PARATYPE: **WO**—1 male, Mt. Karioi, Raglan [37°51'S 174°48'E], 31.viii.–7.ix.1986, malaise tp., Wainui str, H.A. Oliver (BMNH).

Additional material. **AK**—1 male, 10 females, Huia, 4.ix.1969 (NZAC); 1 female, P.D.D., 27.viii.68, B.M. May (NZAC).

Recognition. This species is distinguished by lacking a broad band on wings, lacking dark bands on hindlegs, dark antennae, and first flagellomere nearly twice as long as wide.

Description. Wing length 2.15–2.5 mm.

Male. *Head*: shiny dark brown, dusted with pruinescence; postocellar bristle shorter than ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle two-thirds length of outer bristle; postocular margin with short setae, not overlapping eye. Scape yellowish, pedicel brown, first flagellomere brown, 1.5× longer than wide, arista brown, shorter than remaining antenna.

Thorax: mesonotum shining dark brown; pleura (except katepisternum), scutellum and postnotum faintly dusted with pruinescence. All bristles dark; acrostichals uniserial, alternate setae divergent. Halter knob pale.

Wing: short and broad; infuscate, broad brown band lacking. R_{2+3} ending near opposite median fork, gently arched to C.

Legs: pale yellow, with apical tarsomere darkened. Hindleg lacking dark bands.

Abdomen: dark brown; lateral margins of sternite 7 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 10,11): phallus flanked by postgonites with bifid apex, subequal in length to phallus. Hypandrium lacking flap-like process. Epandrium with anterodorsal lobe with dense setae. Surstylus short, broadly expanded apically, bearing setulae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized, H-shaped, bearing large, spine-like seta; apical lobes long, strongly divergent.

Female. Similar to male except as follows: wing with cloudy infuscation in cell dm and at base of Rs (Fig. 35).

Geographic distribution and seasonal occurrence. This species is known only from the northwestern region of North Island (Fig. 43), and apparently present from late winter to spring.

Icasma fascipennis n.sp.

Figs 12–14, 31, 36, 43

Type material. HOLOTYPE male, "NEW ZEALAND BR/ Mt Sewell/ TV Station, 853 m/ 22 Nov 1984/ B.A. Holloway"; "HOLOTYPE/ Icasma/ fascipennis/ Sinclair [red label]" (NZAC). PARATYPES: **BR**—10 males, 18 females, Mt. Sewell [42°25'S 171°20'E], TV Station, 853 m, 22.xi.1984, B.A. Holloway (NZAC); 2 males, 2 females, same data (CNC); **WD**—1 male, 1 female, Mt. Greenland [44°39'S 168°41'E], 2500', 6.i.1943, E.S. Gourlay (NZAC).

Additional material. **FD**—2 females, Secretary Is., sweeping shoreline, 25.xi.1981, C.F. Butcher (NZAC). These specimens have mostly pale hind legs and I am reluctant to include them as paratypes until associated males are collected.

Recognition. Distinguished from all other species of *Icasma* by a broad band extending across the full width of the wing, dark brown hind femur, with yellow apex, and dark brown hind tibia dark with yellow base.

Description. Wing length 2.1–2.6 mm.

Male. *Head*: dark brown densely covered with grey pruinescence; postocellar bristle shorter than ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle very short; postocular margin with long setae, overlapping eye. Antenna yellowish-brown; first flagellomere slightly longer than wide; arista dark, longer than remaining antenna.

Thorax (Fig. 31): mesonotum shining dark brown, except for median pruinescent stripe, expanding laterally on prescutellar depression; pleura, notopleuron, scutellum, and postnotum faintly dusted with pruinescence. All bristles dark; acrostichals biserial or uniserial, alternate setae divergent. Halter knob dark.

Wing (Fig. 36): short and broad; broad brown band across full width of wing; extending from near base of Rs to base of median fork. R_{2+3} ending just short of median fork, strongly arched to C.

Legs: coxae, trochanters and first tarsomere pale yellow, remaining tarsomeres dark; femora mostly brown with apical fifth pale; tibiae mostly brown with basal fifth and posteroapical comb pale.

Abdomen: dark brown; lateral margins of sternites 7 and 8 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 12,13): hypandrium lacking flap-like process; apex expanded about phallus; postgonites inconspicuous. Epandrium with narrow anterodorsal lobe, bearing setulae. Surstylus long, slender, expanding apically, bearing slender setae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized, apical half fused medially, bearing large, spine-like seta; divided apically into 2 short divergent lobes; lower half divided into widely divergent lobes.

Female. Similar to male.

Geographic distribution and seasonal occurrence. This species is confined to South Island (Fig. 43), collected in late spring and summer.

Etymology. The species name is an adjective derived from the Latin *fascia* (band) and *penna* (wing) in reference to the broadly banded wings.

Icasma longicauda n.sp.

Figs 15,16, 42

Type material. HOLOTYPE male, "NEW ZEALAND: NN/ NW Nelson For. Pk./ Mt.Arthur Tableland/ 17.ii.1995, 950 m/ Quartz Ck., yellow/ pans, B.J. Sinclair"; "HOLOTYPE/ Icasma/ longicauda/ Sinclair [red label]" (NZAC).

Recognition. This species is distinguished by its clear wings, shiny mesonotum (pruinescence confined to scutellum) and unbanded hindlegs. It is most similar to *I. aequabilis* but may be distinguished by features described in the key.

Description. Wing length 2.1 mm.

Male. *Head*: dark brown, clothed in pruinescence, except area at posterolateral margin of ocellar triangle; postocellar bristle shorter than ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle two-thirds length of outer bristle; postocular margin with short setae, not overlapping eye. All antennal segments white; first flagellomere slightly longer than wide; arista pale, base white, longer than remaining antenna.

Thorax: mesonotum shining dark brown; pleura, scutellum, and postnotum faintly dusted with pruinescence. All bristles pale; acrostichals uniserial, alternate setae divergent. Halter knob white.

Wing: short and broad; broad brown band lacking. R_{2+3} ending near base of median fork, gradually arched to C.

Legs: coxae and femora white, remaining segments pale yellow; dark bands lacking on hindleg.

Abdomen: light brown; lateral margins of sternite 7 heavily sclerotized; tergite 8 widely divided medially into pair of rectangular sclerites.

Terminalia (Figs 15,16): phallus flanked by pair of long, thinly sclerotized postgonites extending beyond phallus. Hypandrium with slender apical process, associated with apex of phallus. Epandrium with broad anterodorsal, setose ridge. Surstylus gradually tapering to broad apex, bearing setulae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized, divided narrowly into pair of parallel lobes, bearing long spine-like seta; lower half reduced to short, divergent lobes.

Female. Unknown.

Geographic distribution and seasonal occurrence. Known only from the type locality (Fig. 42).

Biology. This species was collected in yellow pans distributed along Quartz Creek at Flora Hut. This darkly shaded creek was flowing slowly with several small cascades.

Etymology. The species name is a noun derived from the Latin *longus* (long) and *cauda* (tail) in reference to the long postgonites flanking the phallus.

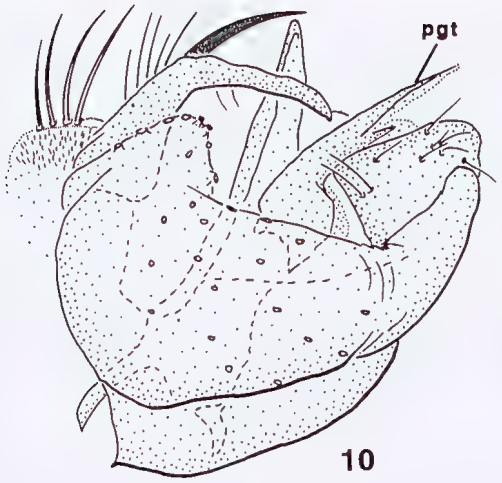
Icasma setosa n.sp.

Figs 8,9, 17,18, 29,30,32, 37, 43

Type material. HOLOTYPE male, "NEW ZEALAND: NN/ Abel Tasman NP, 800 m/ Harwoods Hole sphagnum/ *Nothofagus*, 6–7.ii.1995/ yellow pans,BJ Sinclair"; "HOLOTYPE/ Icasma/ setosa/ Sinclair [red label]" (NZAC). PARATYPES: **BR**—1 female, L. Brunner, Moana Scenic Res., Podocarp, 14–15.ii.1995, yellow pans, B.J. Sinclair (CNC); 10 males, 1 female, Nelson Lakes NP, Lake Rotoiti, 15–16.ii.1995, *Nothofagus* for., B.J. Sinclair (AMS, CNC); **NN**—10 males, 5 females, Canaan, Harwoods Hole, 762 m, 1.ii.1978, A.K. Walker (NZAC); 43 males, 32 females, same data as holotype, yellow pans/sweeping (AMS, BMNH, CNC, NZAC); **WD**—1 male, 1 female, Westland NP, Franz Josef Glacier, 2.i.1984, L. Masner (CNC).

Recognition. This species is distinguished by a broad infuscate band on the wing, extending from R_{2+3} to just beyond cell dm, a shiny scutum (pruinescence confined to scutellum), and banded hindlegs.

Description. Wing length 2.1–2.5 mm.



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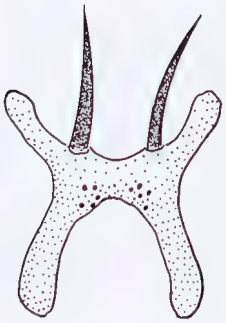

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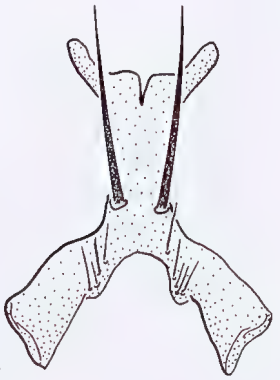

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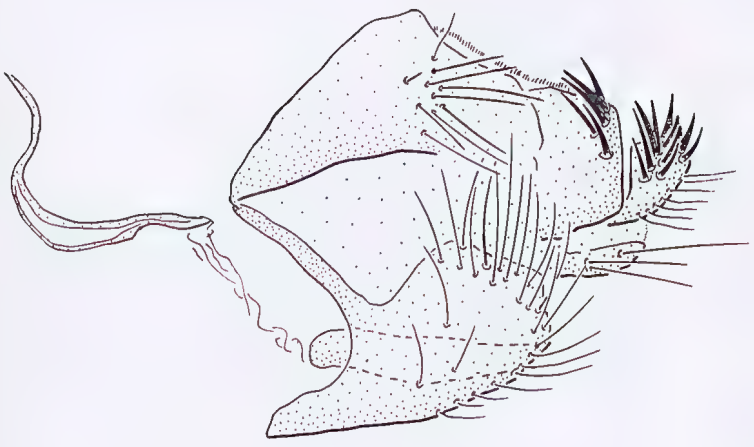

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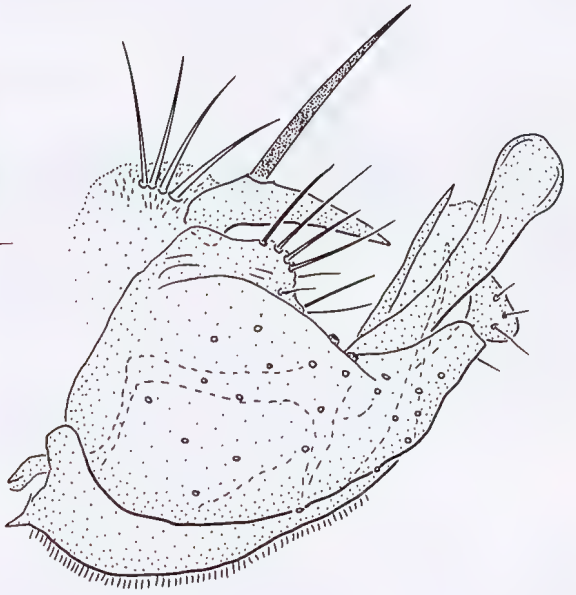

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Figs 10–16. **10**, *Icasma aequabilis*, male terminalia. **11**, *I. aequabilis*, male cercus, anterior view. **12**, *I. fascipennis*, male cercus, anterior view. **13**, *I. fascipennis*, male terminalia. **14**, *I. fascipennis*, female terminalia. **15**, *I. longicauda*, male cercus, anterior view. **16**, *I. longicauda*, male terminalia. Abbreviation: pgt, postgonite.

Male. *Head*: dark brown, faintly dusted with pruinescence; postocellar bristle shorter than ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle two-thirds length of outer bristle; postocular margin with short setae, not overlapping eye. All antennal segments pale yellow; length of first flagellomere nearly twice width; arista dark, longer than remaining antenna.

Thorax (Fig. 32): mesonotum shining dark brown; pleura (except posterior half of katepisternum), scutellum, and postnotum faintly dusted with pruinescence. All bristles dark; acrostichals uniserial, alternate setae divergent. Halter knob dark.

Wing (Fig. 37): short and broad; broad brown band across base, extending from slightly anterior to R_{2+3} to posteriorly beyond cell dm. R_{2+3} ending short of median fork, gradually arched to C.

Legs: pale yellow, with apical tarsomere very dark. Hind femur with wide, median, dark band; hind tibia with corresponding dark band.

Abdomen: light brown; lateral margins of sternites 7 and 8 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 17,18): postgonite tapering to narrow apex, nearly subequal in length to phallus; hypandrium lacking flap-like process; apex expanded about phallus. Epandrium expanded with broad lobe at base of cercus, bearing long setae. Surstylus short, expanding apically, bearing stout apical setae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized separated by deep notch, bearing large, spine-like bristle.

Female. Similar to male except as follows: first flagellomere light brown.

Geographic distribution and seasonal occurrence. This species is confined to South Island (Fig. 43), collected during the summer months.

Etymology. The species name is derived from the Latin *setosus* (bristly) in reference to long setae on the tip of the surstylus.

Icasma singularis Collin

Figs 19, 20, 38, 42

Icasma singularis Collin, 1928: 23.

Type material. LECTOTYPE (here designated) male, "Type/ male [red bordered circle]"; "Icasma/ singularis/ TYPE male Collin [hand written]"; "Icasma/ singularis/ _ [orange circle]"; "N[ew]. Zealand/ Ohakune/ III.1923/ T.R. Harris [hand written]" (BMNH). Paralectotypes: 3 females, same data as lectotype (BMNH); 1 male, Ohakune, 1–9.iv.1923, T.R. Harris (BMNH).

Additional material. **AK**—2 males, 1 female, Huia, 4.v.1969, v.1975 (NZAC); **HB**—1 female, Puketitiri, Little Bush, 20.iv.1982 (NZAC). **NN**—1 male, Spooners Range [41°29'S 172°54'E], Nelson, 1800', 18.iii.1966 (NZAC). **RI**—1 male, Tongariro NP, Ohakune, Mangawhero R., 19–20.ii.1995 (CNC); 1 female, Tongariro NP, 7.5 km N Ohakune, Blythe Tr., 19.ii.1995, *Nothofagus* (CNC). **SD**—3 males, Titirangi, light tp, 9,14.vi.1953 (NZAC).

Recognition. This species is recognised by a broad, dark band, extending nearly across the wing, lack of dark bands on the hindlegs, and yellow antennae.

Description. Wing length 2.0–2.5 mm.

Male. *Head*: shiny dark brown, with scattered pruinescence; postocellar bristle shorter than ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle two-thirds length of outer bristle; postocular margin with short setae, not overlapping eye. All antennal segments pale yellow; length of first flagellomere nearly twice width; arista dark, longer than remaining antenna.

Thorax: mesonotum shining dark brown; pleura, scutellum, and postnotum faintly dusted with pruinescence. All bristles pale; acrostichals biserial. Halter knob yellowish brown.

Wing (Fig. 38): short and broad; broad brown band near base, extending from C to beyond cell dm; remainder of wing infuscate. R_{2+3} ending well short of median fork, arched to C.

Legs: pale yellow, with apical tarsomere darkened. Hindleg lacking dark bands.

Abdomen: light brown; lateral margins of sternite 7 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 19,20): postgonite broad, divergent lobes; hypandrium with flap-like process expanded about phallus and postgonites. Epandrium with very long, stout setae, especially at base of cercus. Surstylus long, slender and strongly arched, expanded apically bearing setulae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized, bearing large, spine-like seta; apical lobes closely approximated, tips divergent.

Female. Similar to male.

Geographic distribution and seasonal occurrence. This species is widespread throughout North Island and northern South Island (Fig. 42). Adults are present from February to June (Plant, 1990; pers. obs.), and have been swept from low vegetation in upland forests.

Icasma tararua n.sp.

Figs 21,22, 33, 39,40, 42

Type material. HOLOTYPE male, "NEW ZEALAND WN/ Tararua Ra/ Dundas Hut Ridge/ 990 m/ 4–6 Dec 1984/ B.G.Bennett &/ T.K.Crosby/ Malaise trap"; "HOLOTYPE/ Icasma/ tararua/ Sinclair [red label]" (NZAC). PARATYPES: **BR**—1 male, Paparoa Range, Buckland Peaks [41°48'S 171°38'E], 25.xi.1984, B.A. Holloway (NZAC); 1 male, 2 females, Mt. Sewell, TV Station, 853 m, 22.xi.1984, B.A. Holloway (NZAC); **FD**—1 female, Secretary Is., 25.v.1981, C.F. Butcher (NZAC); 1 male, Takahe Valley [45°17'S 167°40'E], L. Orbell, 6.xii.1972, A.C. Eyles (NZAC); **NC**—2 males, Arthurs Pass, 3000', 16.xii.1959, J.I. Townsend & J.S. Dugdale (NZAC); **NN**—1 male, 4 females, NW Nelson For. Pk., Mt. Domett, 1067–1219 m, xi.1971, G.W. Ramsey (NZAC); **TK**—1 male, Pouakai Trig., Pouakai Range, 1280–1370 m, 3.xii.1975, J.S. Dugdale & G.W. Mason (NZAC); 6 males, 4 females, Pouakai Range, 1220 m, 9–13.i.1978, malaise tp., J.S. Dugdale (NZAC); **WN**—20 males, 15 females, Tararua Range, Dundas Hut Ridge, [40°44'S 175°27'E], 990 m, malaise tp., 30.xi.–6.xii.1984, B.G. Bennett & T.K. Crosby (NZAC); 3 males, Tararua Range, Dundas Hut, 1250 m, malaise tp., 28–29.xi.1984, B.G. Bennett & T.K. Crosby (NZAC, 3 males, 3 females deposited in each of AMS and CNC); **WO**—1 male, Mt. Pirongia, 962 m, 16.i.1977, A. Walker (NZAC). 3 males, 3 females, paratypes deposited in each of AMS and CNC.

Recognition. Distinguished from other species of *Icasma* by complete pruinescence of the head and mesonotum. Female wings are darkly banded, while the wings of males are clear.

Description. Wing length 1.9–2.6 mm.

Male. *Head*: dark brown, dusted with grey pruinescence; postocellar bristle nearly equal in length to ocellar bristle; outer vertical bristle subequal in length to ocellar bristle and lateroclinate over eye; inner vertical bristle half length of outer; postocular margin with short setae, not overlapping eye. Scape yellow, pedicel yellow; first flagellomere brown, slightly longer than width; arista dark, longer than remaining antenna.

Thorax (Fig. 33): yellowish brown, mesonotum, postnotum, and pleura dusted entirely with pruinescence. All bristles dark; acrostichals uniserial, alternate setae divergent. Halter knob yellowish brown.

Wing (Fig. 39): short and broad; broad brown band lacking, infuscate. R_{2+3} ending opposite median fork, strongly arched to C.

Legs: pale yellow, with apical tarsi darkened. Hindleg lacking dark bands.

Abdomen: dark brown; lateral margins of sternite 7 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 21,22): phallus flanked by pair of tapering postgonites; hypandrium lacking flap-like process; apex expanded about phallus. Epandrium with long setae at base of cercus. Lateral margin of surstylus expanded, apex recurved bearing setulae. Cercus subdivided into two sections; basal cercus thinly sclerotized, surrounding anus; upper cercus heavily sclerotized, H-shaped, bearing large, spine-like seta; apical lobes short, strongly divergent.

Female. Similar to male except as follows: wings with broad dark band across base, extending from C to beyond cell dm (Fig. 40).

Geographic distribution and seasonal occurrence. This species is present from early to mid summer (November to January) in both North and South islands (Fig. 42).

Etymology. The species is named after the type locality and is indeclinable.

The *Icasma masneri* group

This species group is characterised by long, slender wings, vein R_{2+3} long, extending well beyond middle of wing, and the male cerci divided not fused medially, lacking long spine-like setae. This group includes the single species *I. masneri*.

Icasma masneri n.sp.

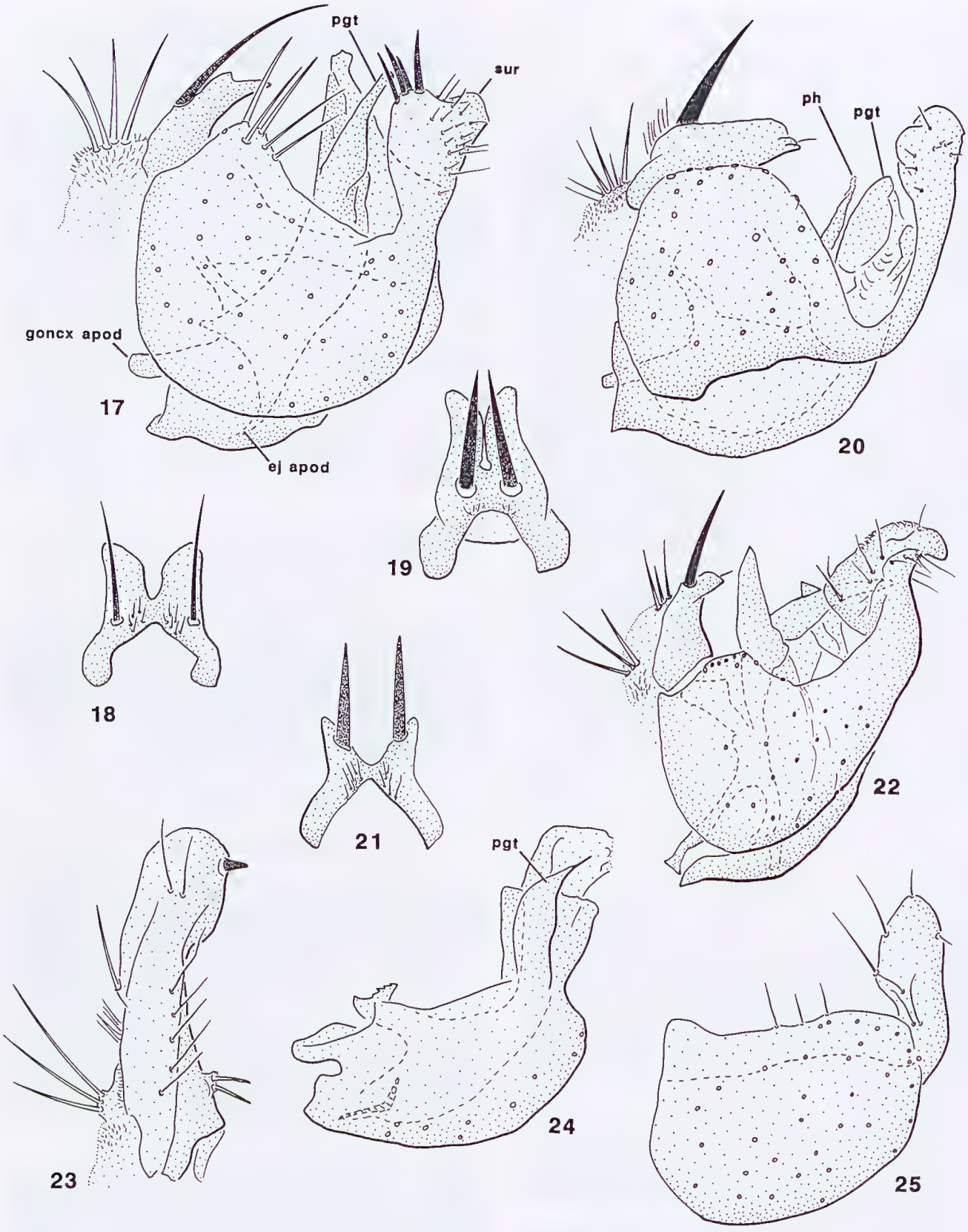
Figs 23–25, 41, 42

Type material. HOLOTYPE male, "NEW ZEALAND: WD/ Westland NP, Franz/ Josef Glacier, yellow/ pans, 10–11.ii.1995/ ex. cascading creek/ B.J. Sinclair"; "HOLOTYPE/ Icasma/ masneri/ Sinclair [red label]" (NZAC). PARATYPES: WD—1 male, Westland NP, Franz Josef Glacier, 2.i.1984, L. Masner (CNC).

Recognition. Distinguished from other species of *Icasma* by clear wings, hind femur with a dark band on the basal half, and scutellum, anterior margin and narrow, median stripe of the scutum clothed in pruinescence.

Description. Wing length 1.8 mm.

Male. *Head*: shiny dark brown, with faintly scattered pruinescence; postocellar bristle equal in length to ocellar bristle; 2 pairs of vertical bristles, outer pair slightly longer and lateroclinate over eye; postocular margin with short setae, not overlapping eye. Scape yellow, pedicel yellow; first flagellomere brown, 1.5× longer than wide; arista dark, longer than remaining antenna.



Figs 17–25. **17**, *Icasma setosa*, male terminalia. **18**, *I. setosa*, male cercus, anterior view. **19**, *I. singularis*, male cercus, anterior view. **20**, *I. singularis*, male terminalia. **21**, *I. tararua*, male cercus, anterior view. **22**, *I. tararua*, male terminalia. **23**, *I. masneri*, male cercus, lateral view. **24**, *I. masneri*, hypandrium, phallus. **25**, *I. masneri*, epandrium, surstylus. Abbreviations: ej apod, ejaculatory apodeme; goncx apod, gonocoxal apodeme; pgt, postgonite; ph, phallus.

Thorax: mesonotum shining dark brown, except for median pruinescent stripe; pleura, scutellum, postnotum, anterior margin of scutum including postpronotal lobe, and notopleuron dusted with pruinescence. All bristles dark; acrostichals uniserial, alternate setae divergent. Halter knob white.

Wing (Fig. 41): long and slender; broad brown band absent; wing faintly infuscate. R_{2+3} ending opposite medial fork, gradually arched to C.

Legs: bright yellow, with apical 3 tarsomeres gradually darkened. Hind femur with wide dark band on basal half; hind tibia lacking corresponding band.

Abdomen: dark brown; lateral margins of sternites 7 and 8 heavily sclerotized; tergite 8 divided medially with posterior fringe of long setae.

Terminalia (Figs 23–25): phallus flanked by pair of postgonites tapering to sharp tip; hypandrium lacking flap-like process; apex expanded about phallus. Epandrium not expanded at base of cercus. Surstylus short, with broad round margin. Cercus not subdivided; heavily sclerotized with round apex; posterior margin with subapical peg-like seta.

Female. Unknown.

Geographic distribution and seasonal occurrence. Known only from the type locality (Fig. 42).

Biology. The holotype was collected in a large, cascading creek, flowing beneath the road to the Glacier. The creek was exposed to bright sunshine, with little shade and the emergent rocks were mostly bare, lacking moss.

Etymology. Named in honour of the collector of the paratype who strongly encouraged my collecting efforts in New Zealand.

Phylogenetic considerations

Glyphidopeza appears to be the most primitive ceratomerine genus, retaining several plesiomorphic characters; for example, presence of a cell cu*p* and pseudotracheae. The genus is characterised by a pair of stout ocellar bristles, inserted anterolaterally to the anterior ocellus, and the secondary sexual modification of the first tarsomere of the male midleg. Despite these two characters, *G. longicornis* may warrant generic status on the basis of significant differences from *G. fluviatilis* (e.g., unbranched R_{4+5}; greatly lengthened scape; eye with ommatrichia), which have been used to define other empidoid genera. This decision must await the collection of additional specimens and species. The striking features of *G. longicornis* are due primarily to male secondary sexual characters and may not warrent separate generic status, especially if females are found to be indistinguishable between the two species.

Glyphidopeza is considered the sister group of the *Icasma* + *Ceratomerus* lineage, and this group is monophyletic on the basis of the following characters: absence of pseudotracheae, loss of cell cu*p*, and two veins distally emitted from cell dm. The latter two genera appear to be monophyletic, but the monophyly of *Ceratomerus* remains to be tested. The monophyly of *Icasma* is supported by character states 1 and 2 discussed below.

Reconstructed Phylogeny of the species of *Icasma*. Seven morphological characters were used in the phylogenetic analysis in an attempt to resolve the relationships among the species of *Icasma*. The remaining taxa of the Ceratomerinae are used to represent a generalised outgroup. The Trichopezinae are considered to represent the sister-group to the Ceratomerinae (Cumming & Sinclair, 1996) and are used to help identify the ground plan apomorphies of the subfamily and assist in determining character polarity.

In the following discussion of characters, the italicised words following a character number describe the apomorphic state of the characters being considered. The character numbers correspond to those used in the cladogram (Fig. 44).

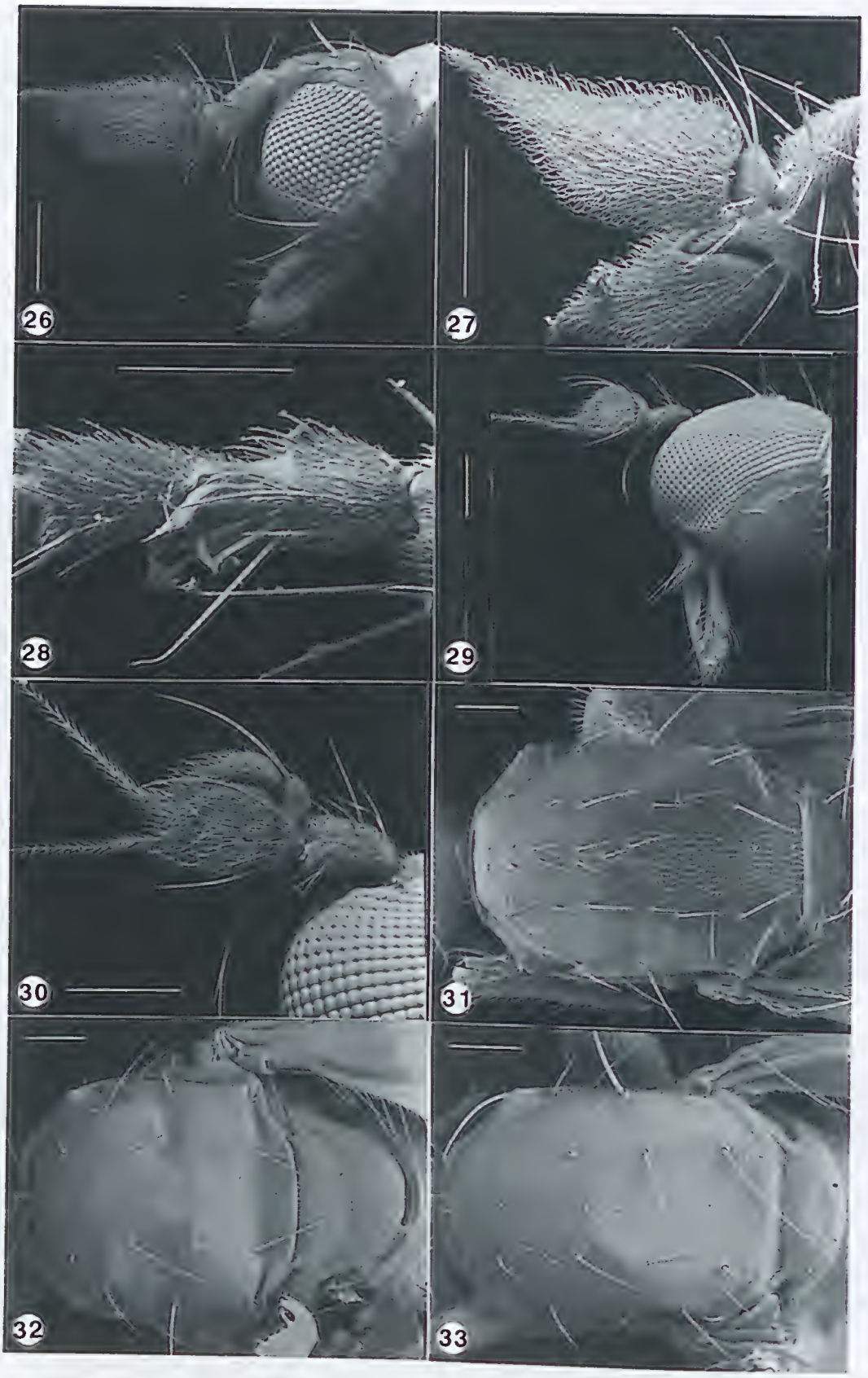
1. *Male cercus heavily sclerotized* The male cercus of the basal genera of the Trichopezinae, *Ceratomerus* and *Glyphidopeza* is normally thinly sclerotized, clothed in setulae and long setae. The cercus of *Icasma* is heavily sclerotized and stout, bearing a pair of modified setae. In contrast to other empidoids with modified male cercus, the cercus of *Icasma* does not appear to be modified for clasping and is quite unique.

2. *R_{4+5} unbranched* R_{4+5} is normally branched in the orthorrhaphous Brachycera, primitive Empidoidea, Trichopezinae, *Glyphidopeza*, and *Ceratomerus*. An unbranched R_{4+5} is also found in the Hybotinae group of subfamilies, Microphorinae, Dolichopodidae, Cyclorrhapha, and numerous genera within the Empidinae, Clinocerinae, and Hemerodromiinae. Despite the obvious homoplastic nature of this character, within the Ceratomerinae an unbranched R_{4+5} is used to characterise the genus *Icasma*.

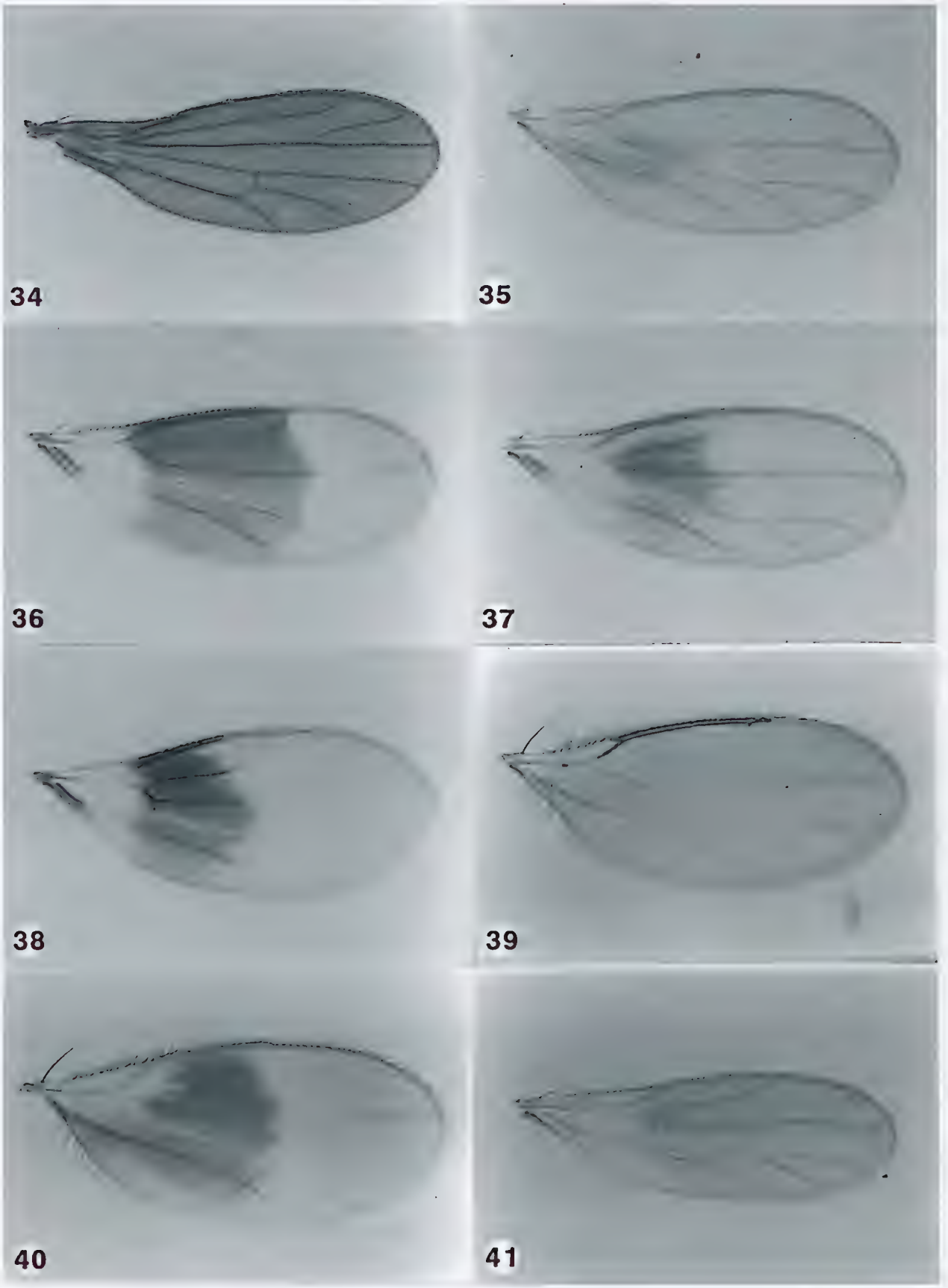
3. *Male cerci fused, bearing pair of long spine-like setae* The male cerci of *Glyphidopeza, Ceratomerus*, and *I. masneri* comprises two separate lobes. The cerci in all remaining species of *Icasma* are narrowly connected ventrally, each bearing a long spine-like seta (Figs 11,12,15).

4. *Wing broad and short* The wing of *Glyphidopeza, Ceratomerus*, and *I. masneri* is long and slender. The *I. singularis* group is distinguished by its broad, short wing (Figs 35–40).

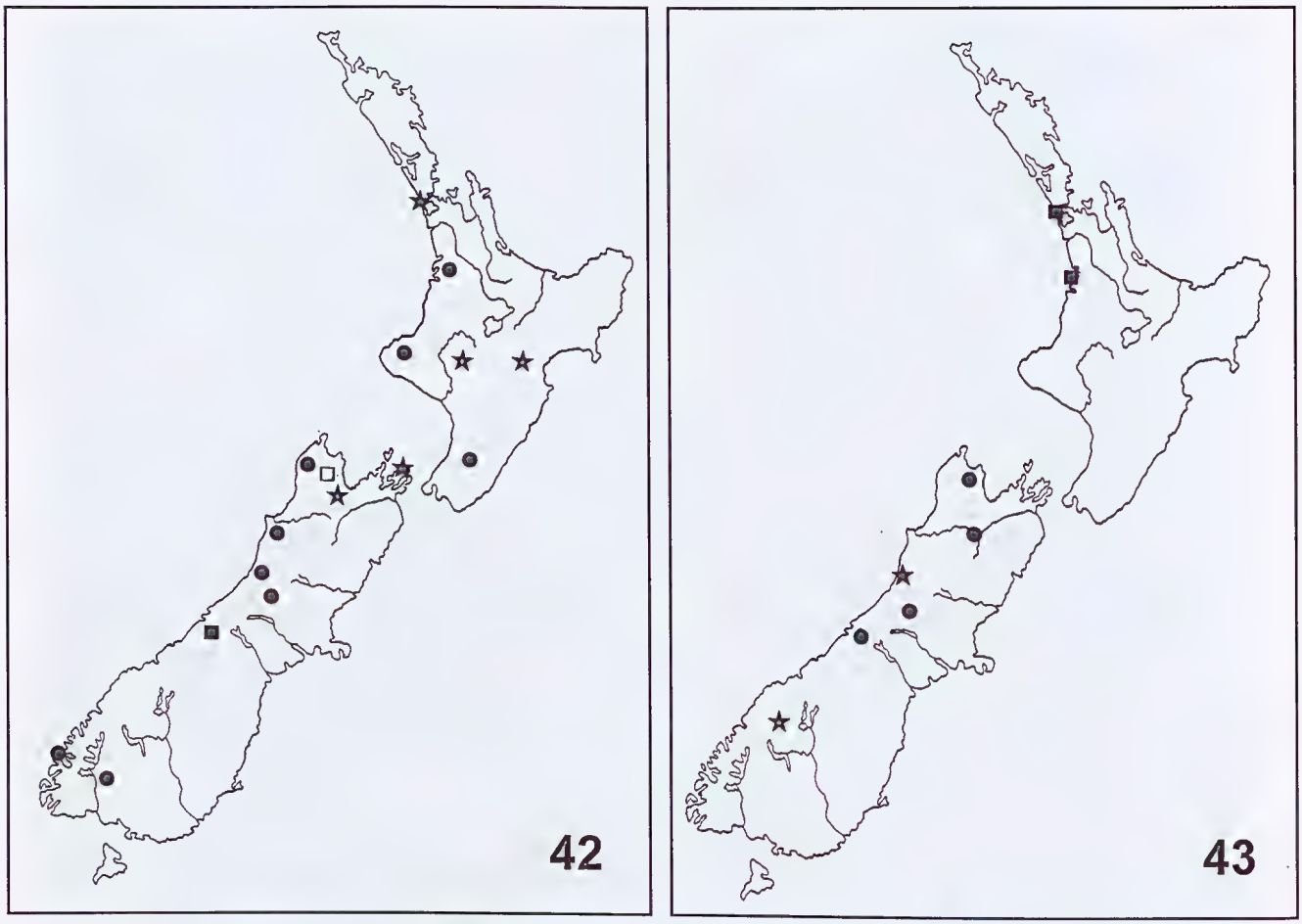
5. *Anterodorsal region of epandrium with dense setae* The anterodorsal region of the epandrium lacks dense setae in *I. masneri* and *I. fascipennis* (Figs 13,25). This region of the epandrium is densely



Figs 26–33. Scanning electron micrographs. **26**, *Glyphidopeza fluviatilis*, head. **27**, *G. fluviatilis*, antenna. **28**, *G. fluviatilis*, first tarsomere, male midleg. **29**, *I. setosa*, head. **30**, *I. setosa*, antennae. **31**, *I. fascipennis*, mesonotum, dorsal view. **32**, *I. setosa*, mesonotum, dorsal view. **33**, *I. tararua*, mesonotum, dorsal view. Scale bars = 0.1 mm, except Fig. 28 where scale bar = 0.05 mm.



Figs 34–41. Left wings of *Glyphidopeza* and *Icasma*. **34**, *G. fluviatilis*. **35**, *I. aequabilis*, female. **36**, *I. fascipennis*. **37**, *I. setosa*. **38**, *I. singularis*. **39**, *I. tararua*, male. **40**, *I. tararua*, female. **41**, *I. masneri*.



Figs 42,43. Known distribution of *Icasma*. **42**, *I. longicauda* (□); *I. masneri* (■); *I. singularis* (★); *I. tararua* (●). **43**, *I. aequabilis* (■); *I. fascipennis* (★); *I. setosa* (●).

clothed with setae in *I. aequabilis* + *I. tararua* and *I. singularis* + *I. longicauda* (Figs 10,16,17).

6. *Surstylus short, broadly expanded apically* The surstylus is short, broadly expanded apically or triangular in profile, supporting the sister-group relationship of *I. aequabilis* and *I. tararua* (Figs 10,22).

7. *Lobes of male cerci closely approximated* The lobes of the cerci are normally widely separated. The lobes of the male cerci are closely approximated in *I. singularis* and *I. longicauda*, supporting their sister-group relationship (Figs 15,19).

The resulting cladogram (Fig. 44) is nearly fully resolved, except for the placement of *I. setosa*.

Zoogeographic considerations

Icasma and *Glyphidopeza* are both apparently endemic to New Zealand. They may still be discovered in southern Chile, but have not yet been found in Australia despite extensive collecting using various mass sampling techniques. If they are found to be truly endemic, this would suggest that both genera evolved following the separation of New Zealand from Australia/Antarctica approximately 84 Mya (Veevers *et al.*, 1991). This scenario of course assumes that their absence is not the result of local extinctions in Australia and Chile.

Glyphidopeza is currently known only from northern South Island. Although *Icasma* is widespread throughout North and South islands, most species are known only from a few localities. Additional distribution data are required before the biogeographic patterns can be investigated. However, the following generalised patterns were found (following the format of Bickel [1991]):

1. North and South islands: *tararua*
2. North Island: *aequabilis*
3. North Island and northern South Island: *singularis*
4. South Island: *fascipennis, longicauda, masneri, setosa*
5. Not recorded from the offshore islands.

Given the scarcity of records in the southern half of South Is., greater collecting efforts (using yellow pans) could result in additional taxa and certainly expand the range of known species.

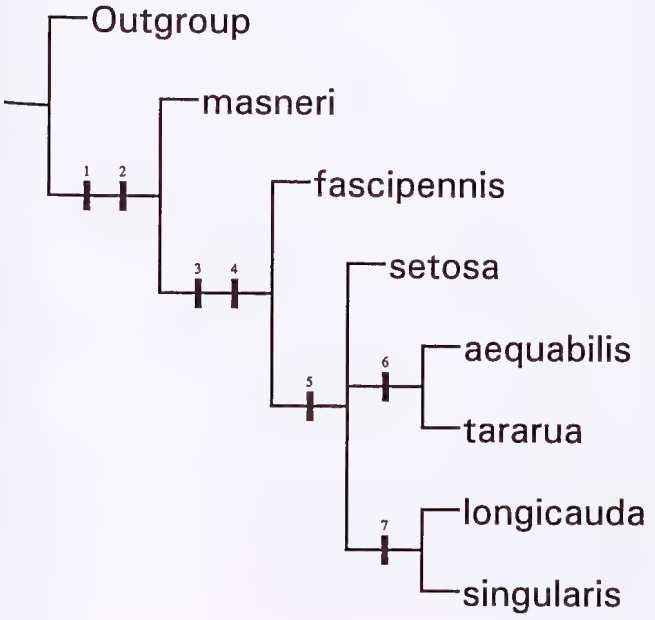


Fig. 44. Hypothesised cladistic relationships of the species of *Icasma*. Numbers refer to characters discussed in "Phylogenetic considerations".

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Compositions of Silver Halides from the Broken Hill District, New South Wales

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Abstract. Some 320 specimens of silver halides from the Broken Hill field, New South Wales, held in the collections of the Australian Museum have been examined. On the basis of colour and habit variations, 42 specimens were selected for analysis. Contrary to previous suggestions, compositions of individual specimens are highly variable and reflect a complex crystallisation history. Bromargyrite has been detected for the first time away from the Broken Hill main lode horizon. Compositions are discussed in terms of the lacunar nature of the appropriate phase diagrams; natural material is shown to reflect compositions of synthetic phases prepared at about 25°C. No obvious relationship between composition and physical properties could be detected for the chlorargyrite-bromargyrite series. This highlights the difficulties of visual identifications.

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The Broken Hill orebody is one of the world's greatest silver-lead-zinc deposits, yet the details of the formation of its oxidised zone are sketchy. The deposit is renowned for its silver halide minerals, which formed the basis of the deposits wealth in its early years. Considerable amounts of bromide and iodide minerals are present, but their extent and relationships to the more common mineral chlorargyrite, AgCl, are not well described. The present work was undertaken to rectify this gap in our knowledge, as part of a larger research programme aimed at developing a fuller understanding of the chemical processes responsible for mineral formation in supergene base metal ores. It is hoped that this will lead to new exploration methods for such deposits and to better extraction processes.

Noteworthy silver halide minerals at Broken Hill, NSW, appear in the oxidised sections of the main lode horizon (Birch *et al.*, 1982; Liversidge, 1886, 1891, 1894; Prior & Spencer, 1902; Smith, 1926) in the Consols Mine (Plimer, 1982) and in the many small silver mines scattered throughout the Broken Hill Block (Stevens, 1980). All three halides were represented in

* Authors arranged alphabetically

the Broken Hill lode: chlorargyrite (AgCl) bromargyrite (AgBr) and the AgI dimorphs iodargyrite and miersite, (end-member compositions are shown). In the main lode, no chlorargyrite (*sensu stricto*) was found (Smith, 1926); it was really bromian chlorargyrite (*var. embolite*), sometimes bearing minor iodine (*var. iodembolite*). Material approaching pure AgCl in composition was only recorded from the Consols Mine and from surrounding deposits in the Broken Hill Block.

A brief comment on nomenclature is warranted here. Birch *et al.* (*op. cit.*) have suggested ranges of compositions for the silver halides but these have no IMA currency. With respect to AgCl-AgBr solid solutions, when Cl and Br predominate, phases are referred to as bromian chlorargyrite and chlorian bromargyrite, respectively. *Embolite* is a varietal name corresponding to a member of the AgCl-AgBr solid solution series. The term *iodembolite* has been used to distinguish similar phases containing, or supposed to contain, significant amounts of iodine. Where mention is made of phases containing all three halogens investigated here, the dominant halide, determines the mineral nature and other halide descriptors are arranged in order of decreasing mol fractions. Thus, bromian iodian chlorargyrite has Cl>Br>I.

Chlorargyrite and bromargyrite form a complete solid solution. Nevertheless, bromargyrite is the rarest of halides from Broken Hill and until this study was unrecorded outside the main lode horizon (Birch *et al., op. cit.*). Complete solid solution of AgI in AgCl and AgBr does not occur at room temperature. Both chlorargyrite and bromargyrite are face-centred cubic and miersite, the body-centred cubic AgI analogue, is unstable with respect to its hexagonal dimorph iodargyrite at ambient temperatures (<146°C). However, the miersite lattice is stabilised at room temperature by solid solution of CuI at amounts greater than about 1 mol% (Barth & Lunde, 1926; Quercigh, 1914; Rolsten, 1961; Spencer, 1901). Complete solid solution exists between miersite and marshite, CuI.

These results were confirmed by Barclay & Jones (1971) in a study of silver halides from Broken Hill and environs, held in the Tate Museum of the University of Adelaide, South Australia. They used X-ray fluorescence methods for the determination of iodine and the application of Vegard's Law to determine chlorine:bromine ratios in minerals, as compared to prepared standards of known composition. Vergard's Law relates the systematic change of unit cell parameters to variations of composition. They also investigated the extent of solid solution AgI in AgCl and AgBr.

While their results broadly agreed with those of earlier workers, several points are raised here. First, their analyses gave constant compositions, or at least average compositions. The question raised is whether large crystals of silver halides, formed over considerable time, would have constant composition; some masses are centimeters in size and compositional variation would be expected to be in line with varying groundwater chemistry (Williams, 1990). Secondly, no attempt was made to relate analyses with physical characteristics of hand specimens. Smith (1926) made several observations relating to apparent comparisons to physical properties such as hardness, sectility and colour. Finally, determinations of the limits of solid solution of AgI in AgCl and AgBr were at odds with other published work (Chateau, 1959a,b,c) and when plotted on an appropriate phase diagram iodine contents of bromian chlorargyrite nowhere approached the solid solution limit in spite of the fact that silver iodides are abundant at Broken Hill intergrown with and growing on the Ag(Cl, Br) phases.

We therefore have determined the compositions of silver halide specimens from Broken Hill and nearby mines using modern SEM EDS X-ray methods, and have related these to the appearance of the minerals (descriptions of colour variations are given in Birch *et al., op. cit.*). Further, we show that these analyses, as well as those of earlier workers lend support to the conclusions of Chateau (*op. cit.*), on the limits of solid solution of the silver halides.

Experimental

Over 320 specimens of silver halides from the Broken Hill, NSW district are held in the collections of the Australian Museum, Sydney, NSW. Each was examined and characterised before 42 were selected for analysis to cover noted physical differences. Most material came from the Broken Hill deposit; two specimens were from the Broken Hill Consols Mine and 11 were from other mines.

The sectility of the halides helped in their preparation for analysis. Samples were pressed in a stainless steel infra-red disc press to give flat surfaces for analysis. No X-ray diffraction measurements were carried out on the silver iodides. Analyses of all identified silver halides (as well as material contained in chlorargyrite and bromargyrite) showed no detectable copper in them. During preparation other phases were not removed from the silver halides, as was done by Barclay & Jones (*op. cit.*). They needed to purify their samples prior to X-ray diffraction measurement; we gained more information by preparation of the whole specimen (*vide infra*).

Specimens were mounted on double sided tape and carbon coated. They were analysed using an Hitachi SEM (model S2500) fitted with the LINK Dispersive System (EDS) AN1000. A 15 kV accelerating voltage was used with a 1 mA beam current. For each analysis spot, 50 second counts were taken using a focused beam. Normally, some 10–12 spot analyses were made for each sample, guidance for which was taken from the brightness of areas detected in back-scattered radiation images. The equipment was calibrated using the VKα peak and analytically pure, laboratory reagent grade AgCl, AgBr and AgI standards were run concurrently with each batch of analyses. Analysed secondary mineral standards used *embolite* (BM83458) and *iodargyrite* (BM84810); numbers in brackets refer to British Museum (Natural History) specimen numbers. Count rates were found to deteriorate on AgI (especially) and other halide standards after several analytical runs, thus requiring repolishing of standards at frequent intervals.

Raw analytical data and SEM-BSE photomicrographs for every spot analysis have been deposited with the Australian Museum, and are available upon request. Elements below a 2σ detection limit are ignored. Several point analyses were made of included accessory minerals such as cerussite. The majority of the analysis of halides approximate well to AgX compositions, although depth of penetration of the electron beam may result in some composites. Extreme high and low totals probably reflect topographic features of the specimen surface, although relative highs of silver analyses versus halides, for example, reflect the presence of native silver in some specimens.

In this discussion, the halide data are normalised to 100% with respect to AgCl+AgBr+AgI and are so reported in the tables below, with a cut-off at a mol fraction of 0.01; this has been chosen as a reasonable limit (i.e., the 1 mol% level) although some analytical data go beyond it. Comparison with other published data on the system shows this cut-off choice does not limit the data or its interpretation.,

Results and discussion

General compositions and attributions. Barclay & Jones (*op. cit.*) suggest that the silver halides of Broken Hill are homogeneously disordered. This would be a natural assumption by extrapolation of their work on the relationship of the compositions of the various solid solution phases to Vegard's Law. This study shows that while their overall limits of solid solution are broadly correct, some natural silver halides from Broken Hill are chemically inhomogeneous; others do have relatively constant composition.

This is illustrated by samples D18759 and D35986 in Tables 1 and 2. The former is an iodian chlorian bromargyrite (*iodembolite*), and the latter a bromian chlorargyrite (*embolite*). Some variation in composition is obvious from the spot analyses, but is not particularly marked. Nevertheless, this differs from specimen D10481 (Table 1), which on bulk analysis is a bromian chlorargyrite. However, one of the spot analyses corresponds to bromargyrite and compositions vary from $AgCl_{0.86}Br_{0.14}$ to $AgCl_{0.21}Br_{0.79}$. Thus, chemical variation of *embolites* cannot be inferred from X-ray powder diffraction measurements. This is not at all surprising. The large masses of silver halides in some specimens could not reflect formation solutions of constant composition since they must have crystallised over a considerable time. Because groundwater compositions are continually changing, the halide composition will reflect that fluctuation in the first order. Thus, the silver halide crystals even millimetres in size would have variable composition reflecting groundwater geochemistries prevailing. All of the analysed silver halides show this variability to different extents.

It should be noted that casual observations of hand specimens are not particularly reliable guides to composition. By way of example, specimen D24260 (Table 1) is labelled as iodargyrite (Table 2). It is a yellow-grey massive material, but the yellowness is not related to the presence of iodine, which was undetected in spot analysis. By way of contrast, bromian chlorargyrite or chlorian bromargyrite *versus* iodine-rich phases are easily distinguished by using back-scattered X-ray images.

Specimens D34811 and D23904 (Table 1) demonstrate the limits of solid solution of the silver halides, in that separate phases are present. In D34811, two phases are apparent in hand specimen (Table 2). The yellow-green phase corresponds to an iodian bromian chlorargyrite near the limit of iodide substitution (*vide infra*). The yellow crystals coating this phase are chlorian iodargyrite with a trace of bromine in one spot analysis. D23904 similarly gave some spot analyses consistent with an iodian *embolite* and four others corresponding with chlorian iodargyrite or pure iodargyrite. What is significant is that D34811 has clearly identifiable yellow-green *embolite* masses dusted by iodargyrite. In contrast, D23904 appears in hand specimen to be a single phase in terms of colour. Only detailed analysis can reveal the admixture of several phases.

Iodembolites. *Iodembolite* was a term given to bromian chlorargyrite bearing a small amount of iodine. It was apparently distinguished from *embolite* (or simple bromian chlorargyrite) by its greenish to orange-yellow colour, and hardness and sectility differences (Birch *et al., op. cit.*). Twelve specimens from the Australian Museum, labelled "iodembolite", have been analysed. Visual methods used to distinguish such silver halides are unreliable.

D23904 and D18759 (Tables 1 and 2) were both labelled "embolite". The former, even though including an AgI phase, bears considerable iodine and would fit its name. However, the latter is clearly an iodian chlorian bromargyrite. Both are waxy, yellowish green to green halide. Analyses of the remaining ten *iodembolites* are given in Table 3. Most were yellowish green or green, some purple or greenish brown and others were black as a result of photochemical alteration of the surface.

Three groups of analysis are evident. The first (D25918, D28196, D29303 and D29383) corresponds to bromian chlorargyrite with no iodine detected, although one spot analysis in D29383 corresponds to chlorian iodargyrite. Other analyses in D29383 place it close to bromargyrite. Four analysis (Table 3) correspond to halides in which small amounts of iodine are occasionally determined (D20648, D25951, D26980 and D28194). In D20648, pure iodargyrite and bromian iodargyrite are present as well, as separate phases. As no iodine was detected in a number of spot analyses for this specimen (and for D29383), the iodide phase probably crystallised during a separate mineralising event. Otherwise, the bromian chlorargyrite would be saturated with iodide. Finally, two *iodembolites*, D30448 and D31586 (Table 3), contain more iodine and it was found in most of the spot analyses. Both these phases appear to be homogeneous in lacking separate AgI (see descriptions of *iodembolite* in Table 2).

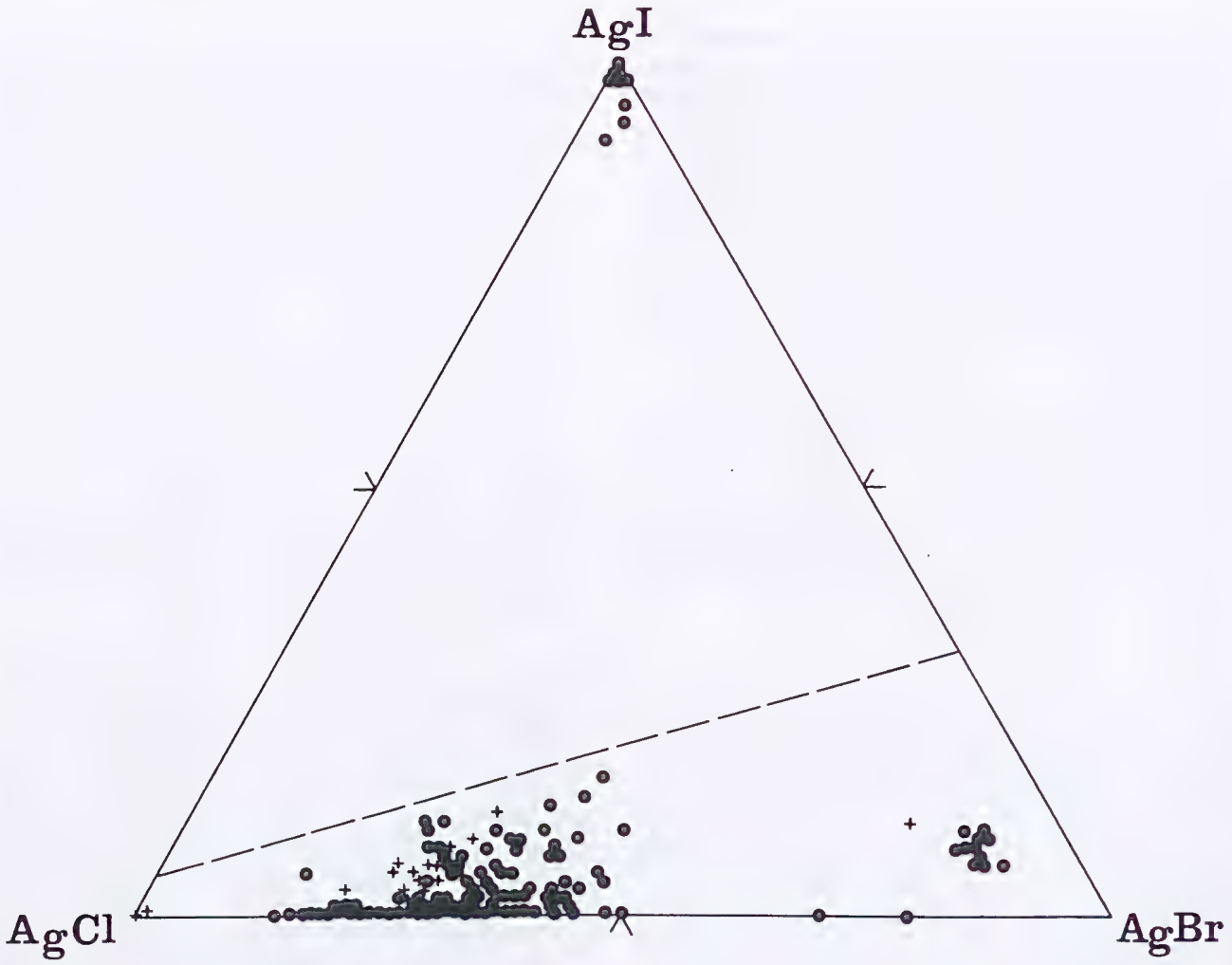

Fig. 1. Compositions of all silver halide specimens (spot analyses) from the Broken Hill main lode horizons (filled circles), together with the average data (crosses) for specimens analysed by Barclay & Jones (*op. cit.*). No locality data were provided for the latter specimens. The dashed line joins the experimentally determined limits of solid solution of AgI in AgCl and AgBr at 25°C (Chateau, *op. cit.*).

Embolite. Bromian chlorargyrite is most commonly associated with Broken Hill (Birch *et al., op. cit.*). Thirteen Australian Museum samples have been analysed in this study (Tables 1 and 4). Relating compositions, colour, association, etc. (Table 2) has proved just as problematic as for *iodembolites*. In some cases the names would appear to be interchangeable. Colours vary from purple-brown to yellow, greenish yellow and green.

The two *embolite* analyses in Table 1 illustrate this point. D35986 has an ideal composition for the mineral, but two halide phases are present. Purple-brown material is coated by a second generation of waxy, green, reticulated halide. No significant compositional difference between the two generations of bromian chlorargyrite could be detected. By way of contrast, D34811 also carries two distinguishable halide phases, yellow iodian bromian chlorargyrite (*iodembolite*) coated with minute, canary yellow crystals of iodargyrite. Remaining analyses of "embolites" reveal that they are either bromian chlorargyrites alone, or with minor amounts of iodine in substitution. Analyses are not indicative of homogeneous materials, with bromine mol fractions varying from 0.2 to 0.4. Some analyses more closely approach bromargyrite. One spot analysis in D29370 indicates patches of chlorian bromargyrite embedded in bromian chlorargyrite. Attention is drawn here to specimen D36399. Coronadite gossan forms the matrix, on which greenish-yellow, crystalline halide is coated with masses of a later, bright yellow phase. The two are obviously the result of separate mineralising events with the greenish material corresponding to approximately $AgCl_{0.7}Br_{0.3}$ with a trace of iodine in one analysis, and the bright yellow material to AgI with trace amounts of chlorine. Similarly, in D35996 and D34495, chlorian bromian iodargyrite is embedded in a groundmass of green *embolite* veinlets in kaolin.

Other attributions. *Bromyrite* (bromargyrite) is a rare mineral from the oxidised zone of the Broken Hill orebody (Birch *et al., op. cit.*; Barclay & Jones, *op. cit.*), although silver halides within the *embolite* range sometimes show spot analyses corresponding to

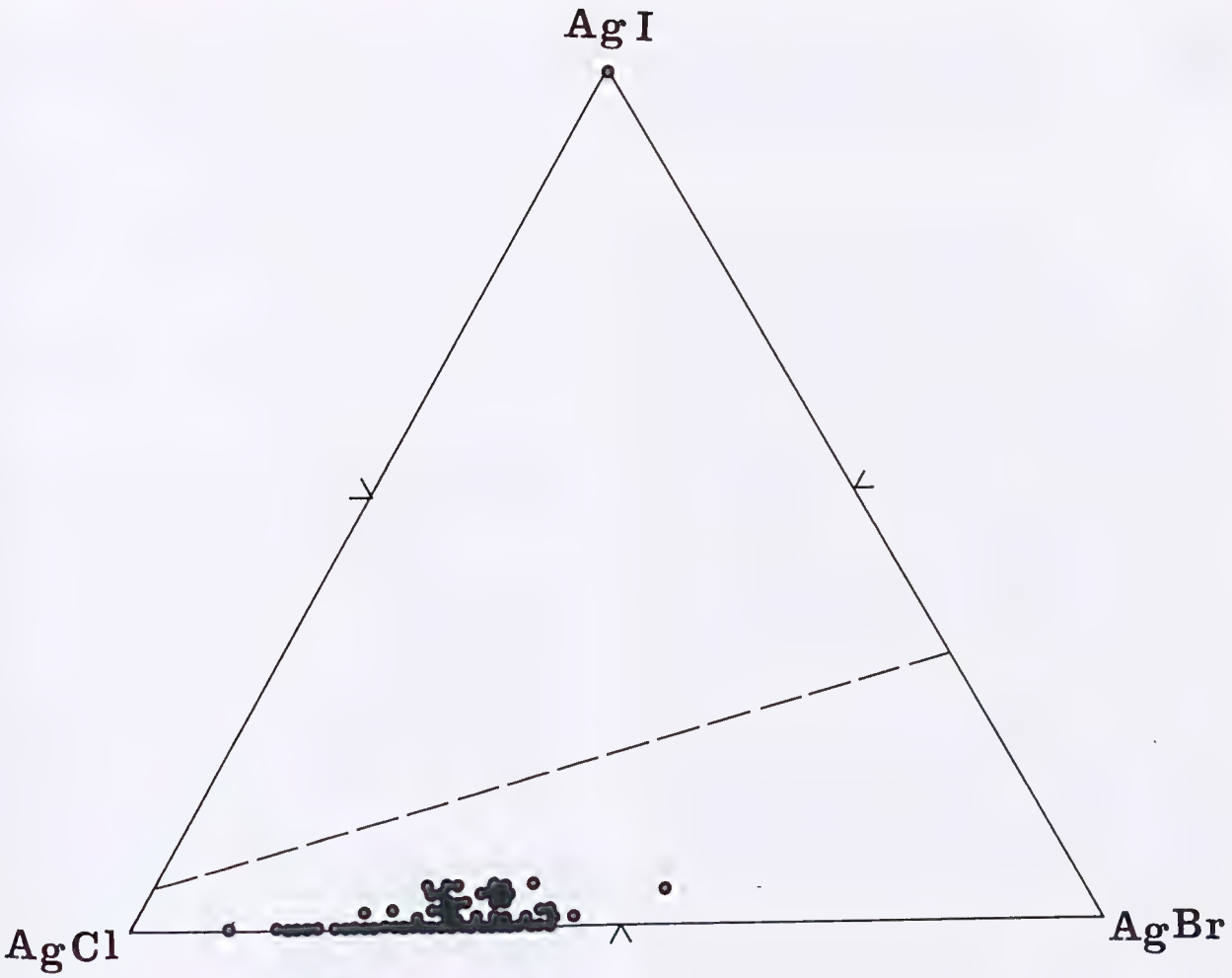

Fig. 2. Compositions of silver halides as reported in Figure 1 for specimens collected from deposits remote from the Broken Hill main lode horizons.

bromargyrite (*sensu stricto*). Reference to Table 1 reveals that confusion remains concerning visual identification of bromargyrite. Specimen D18759 is an iodian chlorian bromargyrite but was labelled "bromyrite" and relabelled "iodembolite" (Table 2). While it is gratifying to report another true bromargyrite from Broken Hill, it shows the problems of unchecked attribution. One of the four analysed specimens (Table 5; D46338) is purportedly a bromargyrite. It is yellow, but is an iodian bromian chlorargyrite. None of the spot analyses approaches the attribution, but the iodine contents of the solid solution series in this case are significant. Comments on colour identification of bromargyrite (Birch *et al., op. cit.*) need modification in the light of the analytical data presented here.

Specimens labelled "cerargyrite" (chlorargyrite) are similarly bedevilled by mis-attribution since such specimens contain significant bromine and iodine. It was previously reported that specimens from the Broken Hill Consols Mine approach the end member in composition (Barclay & Jones, *op. cit.*; Birch *et al., op. cit.*; Plimer, *op. cit.*). D10481 (Table 1) and D26168 (Table 5) are *embolites*, the latter with a trace of iodine. Analyses of *cerargyrites* from the Broken Hill Consols Mine (Table 5) also reveal incorrect attribution. D28184 is an unexceptional *iodembolite* while D28185 contains significant iodine and bromine. This gives no support to the contention that the Consols Mine halides are more chlorine-rich than those derived from the main lode horizons.

Aside from pieces or fragments of gossan included in the silver halides, native silver and fragments or crystals of cerussite, $PbCO_3$, are also encountered. Some point analyses are worthy of comment. In a few specimens, isolated grains give high lead **and** chlorine values, but low silver. They could not be attributed to cerussite but may correspond to phosgenite, $Pb_2CO_3Cl_2$, a mineral reported in the district only from the Broken Hill Consols Mine (Birch *et al., op. cit.*; Plimer, *op. cit.*) There it was found with cerussite, vanadinite, $Pb_5(VO_4)_3Cl$, and chlorargyrite. Alternatively, the grains might be cotunnite ($PbCl_2$), the Pb(II) oxy- or hydroxychlorides laurionite or

paralaurionite, (PbOHCl), mendipite ($Pb_3O_2Cl_2$) or other related species (Edwards *et al.,* 1992). These grains were, however, too small to separate for X-ray identification. Thus a careful search for these halide specimens, now underway, may turn up such species new to Broken Hill.

In the main lode (*vide infra*), silver iodide is common as inclusions or intergrowths with bromian chlorargyrite (unlike specimens in the surrounding district). This may only be revealed in the back-scattered electron images of prepared specimens, as confirmed by subsequent analysis. Two modes of occurrence or patterns of halide distribution are noted. The first concerns AgI associated with bromian chlorargyrite of low iodine content, with the AgI formed in an earlier separate mineralising event and simply enclosed by the later, iodine-deficient phase (see D20648). Alternatively, where AgI is detected together with iodian bromian chlorargyrite with elevated iodine content, the two phases grew together as a result of the hosting bromian chlorargyrite phase reaching the limit of solid solution with silver iodide (see D34811).

Silver halides from other Barrier Range deposits. Halides from mines distant from the main Broken Hill orebody are analysed in Table 6 and described in Table 7. Individual spot analyses are shown in Figure 2.

Many of the observations on halides from the Broken Hill main lode are mirrored in these specimens. Compositional variation is, for example, quite pronounced. Samples D30480, D30482 and D30484 are all from the Model Republic Mine at Purnamoota. D30480 is an iodian bromian chlorargyrite of constant composition around $AgCl_{0.60}Br_{0.35}I_{0.05}$. While all these are *iodembolites*, the other specimens have quite variable iodide contents and chloride mol fractions vary from 0.54 to 0.84. Specimen D35460 from the Caledonian Mine, Purnamoota is more varied. Five spot analyses correspond to bromian chlorargyrite or *iodembolite*. However, one analysis corresponds to an iodian chlorian bromargyrite indicating that some of the mass crystallised from an aqueous solution with elevated bromide activities. This analysis represents the first report of a bromargyrite in the Broken Hill Block, away from the Broken Hill main lode.

All other samples analysed correspond to bromian chlorargyrite (*embolite*) or *iodembolite*, little different to those from the main lode. However, in some support of the observation by Smith (1926) that chlorargyrite was typical of the Consols Mine and others outside the main lode area, one spot analysis from the Maybell North Mine, Mount Gipps, gave the highest proportion of chloride amongst other material analysed in this study, $AgCl_{0.90}Br_{0.10}$.

Reference to Figure 2 shows that analyses of halides from outside mines are comparable to those from the Broken Hill lode, in terms of Cl:Br ratios. One noticeable difference is less iodine in the more remote localities, although crystals of pure AgI are found in gossans from Little Darling Creek, Mookaie Hill and Mulga Springs (N. Gray and P.A. Williams, unpublished results).

Finally for this group of halides, mention should be made of mineral inclusions other than gossan pieces (as in D35460). Cerussite occurs in samples from the Maybell North and Day Dream Mines. Some alteration to native silver is detected in D18719; native silver is pronounced in hand specimen. Two spot analysis of an inclusion in D30480 from the Model Republic Mine correspond to pure Ag_2S; although it is not known whether the sulfide phase is primary or secondary, it clearly alters to the halide.

Limits of solid solution in the silver halides. Reference to Figures 1 and 2 shows that silver halides from the Broken Hill field are quite variable in chloride:bromide:iodide ratios, both in the main lode horizons and more remote localities. Chlorargyrite is the dominant species, as might be expected given normal geochemical distributions (Williams, *op. cit.*) that suggest compositions with Cl>Br>I would dominate. However, the high amounts of Br and I in the silver halide suites from Broken Hill and environs are both noteworthy and unexplained. Groundwater chemistries compatible with observed compositions of mineral suites must have prevailed.

Aside from this, it is worth examining the extent of solid solution in the silver halides, both from analysis and laboratory studies of synthetic materials. Barclay & Jones (*op. cit.*) investigated the limits of solid solution of AgI in the AgCl and AgBr. Unfortunately, their report appears to be in error because of computational matters and other, unconstrained variables. The latter centre about the fact that the solid solution experiments performed were not conducted at constant temperature (at least as reported in the literature). Furthermore the limits of solid solution of AgI in the other silver halides, as reported in the appropriate figure, reflect weight percent values, rather than mol percent values, as represented. Recalculation of their data gives limits of solid solution of AgI in the other halides of $AgCl_{0.93}I_{0.07}$ and $AgBr_{0.65}I_{0.35}$. Even with these corrections, we cannot apply them to our considerations as they correspond to undefined temperatures.

Good sense is made of their analytical data, in relation to the work of Chateau (*op. cit.*). He determined limits of solid solution among the silver halides for different reasons to those considered for naturally occurring phases. His results give the extent of solid solution of AgI in AgCl and AgBr as 5 and 31 mol percent, respectively, at 25°C. He also noted that AgCl and AgBr solution in AgI was much more restricted, amounting to less than about 5 mol percent (Chateau, 1959b,c) even at temperatures up to 70°C. These results are not too different to those of Barclay & Jones *(op. cit.)*, who did not specify the temperatures of their experiments.

Extrapolation of solid limits of AgI in AgCl-AgBr solutions (i.e., the ternary system) is not based on

detailed experimental study. However, we can connect the end member solid solution limits (AgI in AgCl or AgBr) as a guide, as shown in Figures 1 and 2. This relationship closely matches compositions of naturally occurring phases. All of the reported analyses for iodian bromian chlorargyrite and bromargyrite analogues fall below the line; substituted silver iodides are observed as separate phases when more iodide was apparently available in mineralising solutions. This accords with the analytical data reported here for specimens which consist of admixtures of ternary phase and AgI.

We note that a temperature of 25°C would most likely correspond to conditions prevailing when these halides were formed; lower temperatures would serve to lower the limits of AgI substitution in AgCl-AgBr solutions. Higher temperatures would, by accommodating more extensive solid solution, not favour the compositions we have found.

Finally, we stress that the silver halides analysed here are anything but homogeneous. These species are substantial masses of largely crystalline material. Therefore they most probably crystallised over an extended period. This explains why the halides are so heterogeneous; groundwater compositions would fluctuate in composition and the chemical nature of the solid phase simply reflects those changing groundwater chemistries.

Detailed examination of spot analyses reveals such changing patterns, in a way that the figures, being an amalgamation of all data, do not. First, the tables show that for many spot analyses, iodine was not detected or was present in only trace amounts. In some specimens, iodine is present in uniformly high amounts. Localised reaction chemistry could explain that, but patterns of AgBr substitution in AgCl are more subtly complex. In *individual* specimens, zones corresponding to, roughly $AgCl_{0.75}Br_{0.25}$, with negligible iodine contents, are part of a single phase of varying composition juxtaposed with zones with approximate composition $AgCl_{0.65}Br_{0.35}$. The latter most frequently contain more iodine. As zones of these compositions are found in many specimens, these patterns of substitution probably represent particular mineralising events. Similarly, the bromargyrite phases belong to yet another, separate mineralising episode. Nevertheless, these minerals are very heterogeneous in composition and this may be overlooked if they are examined by methods related to Vegard's Law properties or if they are classified by physical properties and attributes.

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SUPPLEMENTARY MATERIAL. Descriptions of all of the specimens examined, non-normalised analytical data and back-scattered images showing point analysis locations have been deposited with the Collection Manager of the Mineralogy and Petrology Section, Australian Museum.

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Table 1. Compositions derived from spot analyses of selected specimens of silver halides from Broken Hill.

No.[a]		Composition[b]											
D18759	Cl	8	11	9	8	10	12	10	11	10	11	10	8
	Br	86	83	82	83	84	80	82	81	80	81	83	82
	I	6	6	9	9	6	8	8	8	10	8	7	10
D35986[c]	Cl	67	67	67	68	72	65	68	67	70	68	66	68
	Br	33	33	33	32	28	35	32	33	30	32	34	32
D10481[d]	Cl	69	86	85	55	72	62	30	79	60	68	75	67
	Br	31	14	15	45	28	38	70	21	40	32	25	33
D34811	Cl		1		1	1		1	1	1	63	65	65
	Br					1					26	25	24
	I	100	99	100	99	98	100	99	99	99	11	10	11
D23904[e]	Cl	63	65	63	68	65	65	65	66				
	Br	30	28	30	28	29	30	27	26	2			
	I	7	7	7	4	6	5	8	8	98	100	100	100
D24260[f]	Cl	69	71	73	75	67	72	73	71	67	67	72	81
	Br	31	29	27	25	33	28	27	29	33	33	28	19

[a] Australian Museum specimen number. [b] Compositions expressed in mol% terms; thus, the first analysis for D18759 corresponds to $AgCl_{0.08}Br_{0.86}I_{0.06}$. For specimen descriptions see Table 2. Where no number is reported in the Table, the halogen was not detected during analysis; traces of As detected. [c] Traces of Pb, As, Fe detected. [d] Traces of P detected. [e] Traces of As detected. [f] Traces of Pb, P, As detected.

Table 2. Specimen descriptions for silver halides from the Broken Hill main lode and the Broken Hill Consols Mine.[a]

D18759 LABEL: No.682 Iodembolite changing into native silver, Proprietary, Broken Hill.
LABEL: Iodembolite and native As (*sic*), Broken Hill.
COMMENTS: On the first label, the word "bromyrite" is crossed out and replaced by the word "iodembolite." Sample consists of massive green halide altering to native silver, accompanied by some soft orange clay.

D35986 LABEL: Embolite on matrix, Broken Hill, NSW.
Comment: Ferruginous, manganiferous gossan cementing quartz chips and fragments coated by purple-brown halide, then by later greenish halide in worm-like masses. Both halides were analysed but could not be distinguished.

D10481 LABEL: Cerargyrite on kaolin, Broken Hill, NSW.
COMMENTS: Green halide masses and veinlets in massive kaolinite.

D34811 LABEL: Embolite, Broken Hill, NSW.
COMMENTS: Yellowish halide with minor iron oxyhydroxides with later bright yellow dusting of second generation halide. The latter is iodargyrite, by analysis.

D23904 LABEL: Iodembolite, Broken Hill, NSW.
COMMENTS: Waxy, yellow-green halide globules to 2 mm on porous, hematite gossan.

D24260 LABEL: Iodargyrite, Broken Hill, NSW.
COMMENTS: Waxy, yellow-green, massive halide.

D25918 LABEL: Iodembolite with cerussite, Proprietary Mine, Broken Hill, NSW.
COMMENTS: Halides altered by light exposure to black masses on massive cerussite associated with orange iron oxyhydroxides. Cerussite inclusions were detected in the prepared samples.

D28196 LABEL: Iodembolite, Proprietary Mine, Broken Hill, NSW.
COMMENTS: Well-crystallised yellow-green halides associated with minor iron oxyhydroxides; crystals of bromian chlorargyrites to 2 mm.

D29303 LABEL: Iodembolite in kaolin, Block 11, Proprietary Mine, Broken Hill, NSW.
COMMENTS: Massive white kaolinite matrix bearing small red garnet crystals is impregnated with green halide masses and veinlets; this material was analysed. An open vugh in the specimen contained large (to 5 mm) halide crystals, some of which were coated with a second generation of bright yellow powdery halide.

D29383 LABEL: Iodembolite, Broken Hill, NSW.
COMMENTS: Stalactitic coronadite with later purple halide crystals to 4 mm. X-ray map showed bright patch of AgI and another of a Pb-rich phase.

D20648 LABEL: Iodembolite with smithsonite, Broken Hill, NSW.
COMMENTS: Minor coronadite with clays and iron oxides accompany the bulk of the specimen which consists of an intergrowth of "teardrop" and crystallised smithsonite, cerussite (minor) and yellow-green halide; the smithsonite was last to crystallise.

D25951 LABEL: Iodembolite with iodyrite, Proprietary Mine, Broken Hill, NSW.
COMMENTS: Bright yellow crystalline masses of halide coated by later greenish-yellow to brown colloform halide. Analyses do not distinguish between the different coloured phases; the specimen is dusted by later iron oxyhydroxides.

D26980 LABEL: Iodembolite, Broken Hill, NSW.
Comment: Specimen consists of aggregates of cerussite crystals and some massive cerussite cemented by later yellow-green halide in crystals to 3 mm. X-ray map shows cerussite inclusions in halide.

D28194 LABEL: Iodembolite, Proprietary Mine, Broken Hill, NSW.
COMMENTS: Ferruginous gossan coated with purple-grey material and waxy, green halide masses.

D30448 LABEL: Iodembolite on matrix, Broken Hill, NSW.
COMMENTS: Matrix is rotten, oxidised garnet sandstone containing quartz fragments and siliceous iron-rich gossan bearing yellow crystals of halide on more open, vughy areas and yellow-green masses in cavities; some filiform masses to 1 cm coat the specimen.

D31586 LABEL: Iodembolite, Broken Hill, NSW.
COMMENTS: Slug of halide varying in colour from green to yellow and then to purple-brown.

D29370 LABEL: Embolite, Broken Hill, NSW.
COMMENTS: Matrix is a fine-grained, cerussite-rich, banded material after garnet sandstone coated and impregnated by greenish brown, arborescent masses of halide.

D30466 LABEL: Embolite on kaolin, Broken Hill, NSW.
COMMENTS: Specimen consists of masses of waxy, green halide crystals to 7 mm impregnating a mass of kaolinite bearing minor Mn oxides.

D30481 LABEL: Embolite in kaolin, Broken Hill, NSW.
COMMENTS: Dense, Grey, banded halide associated with minor Fe-stained clay.

D30360 LABEL: Embolite, Broken Hill, NSW.
COMMENTS: Specimen consists of a massive and reticulated crystalline cerussite nodule bearing yellow-green halide crystals in cavities; minor limonite coatings invest parts of the specimen.

D31665 LABEL: Embolite with cerussite and malachite, Broken Hill, NSW.
COMMENTS: Massive cerussite is coated by later purple-grey halide crystals to 2 mm; malachite crystal plates are scattered across both phases.

D36399 LABEL: Embolite, Broken Hill, NSW.
COMMENTS: Matrix of coronadite gossan is coated with yellow-green halide crystals and separate, bright yellow halide masses; both halide phases were analysed separately.

D35996 LABEL: Embolite in kaolin, Broken Hill, NSW.
COMMENTS: Veinlets of green halide invest massive kaolinite.

D33111 LABEL: Broken Hill, NSW.
COMMENTS: Unidentified green copper mineral coats mass of green halides bearing later native copper; base of specimen bears a bright, apple-green species and minor iron oxyhydroxides.

D32138 LABEL: Embolitedendroids, Proprietary Block 14 Mine, Broken hill, NSW (Presented Block 14 Ltd).
COMMENTS: Green dendroidal sheet of halide dusted with powdery blue copper mineral (unidentified).

D29066 LABEL: Embolite with iodyrite in kaolin, Broken Hill, NSW.
COMMENTS: Massive, yellow-green halide.

D34495 LABEL: Embolite, colloform arborescent masses, Broken Hill, NSW.
COMMENTS: Yellow to greenish brown colloform masses of halide associated with minor clays.

D46338 LABEL: Bromyrite, Broken Hill, NSW.
COMMENTS: Aggregates of yellow to bright yellow halide crystals to 3 mm on orange ferruginous gossan.

D26168 LABEL: Cerargyrite in kaolin with malachite, Broken Hill, NSW.
COMMENTS: Green halide masses in kaolinite with red garnets; later dusting of malachite.

D28184 LABEL: Cerargyrite, Consols Mine, Broken Hill, NSW.
COMMENTS: Slug of purple-grey halide with minor quartz inclusions; some halide is crystalline.

D28185 LABEL: Cerargyrite with bromyrite and silver-chloro-antimoniat (*sic*) in limonite, Consols Mine, Broken Hill, NSW.
COMMENTS: Matrix is a ferruginous gossan bearing some compact hematite masses one side of the specimen bears bright yellow halide crystals; the other (analysed) was coated with yellowish green halide crystals to 1.5 mm.

[a] In order of discussion in text; in the Table, "Label:" refers to the specimen description on the Australian Museum label (*verbatim*).

Table 3. Compositions of *iodembolites* from Broken Hill.[a]

No.		Composition												
D25918[b]	Cl	65	61	66	67	68	64	61	64	81	62			
	Br	35	39	34	33	32	36	39	36	19	38			
D28196[c]	Cl	80	66	84	83	68	65	68	73	63	66			
	Br	20	34	16	17	32	35	32	27	37	34			
D29303[d]	Cl	60	60	57	67	67	67	65	66	68	69			
	Br	40	40	43	33	33	33	35	34	32	31			
D29383[e]	Cl	63	50	52	62	63	78	65	66	61	52	62	2	
	Br	37	50	48	38	37	22	35	34	39	48	38		
	I												98	
D20648	Cl	54	78	74	71	77	70	78	74	82	71			
	Br	42	22	26	29	22	29	22	26	18	29			1
	I	4				1	1					100	100	99
D25951[b]	Cl	61	63	60	64	65	67	80	67	64	66	63		
	Br	39	37	40	36	35	33	20	33	36	34	36		
	I											1		
D26980[e]	Cl	78	79	67	61	65	79	61	71	66	76			
	Br	22	20	33	39	35	21	39	29	34	24			
	I		1											
D28194[e]	Cl	64	64	60	65	72	63	76						
	Br	36	36	40	33	26	37	34						
	I				2	2								
D30448[c]	Cl	57	64	61	68	64	59	69	63	66	58	64		
	Br	41	26	37	32	36	39	30	37	34	39	36		
	I	2		2			2	1			3			
D31586[f]	Cl	57	64	61	60	50	47	54	62	62	60	60	67	
	Br	43	34	39	38	46	39	39	38	35	38	38	32	
	I		2		2	4	14	7		3	2	2	1	

[a] Analyses are reported in the same way as in Table 1. [b] Traces of As, Pb, Fe detected. [c] Traces of Pb, Fe detected. [d] Traces S, As, Fe, detected. [e] Traces Fe, As detected. [f] Traces Pb, S, P, As, Fe detected.

Table 4. Analyses of embolites from Broken Hill.[a]

No.		Analyses											
D29370[b]	Cl	60	62	61	63	66	74	66	61	76	19		
	Br	40	38	39	37	34	26	34	39	24	81		
D30446[c]	Cl	71	70	77	76	76	67	76	81	75	67	76	67
	Br	29	30	23	24	24	33	24	19	25	33	24	33
D30481[d]	Cl	64	66	66	68	61	61	68	71				
	Br	36	34	34	32	39	39	32	29				
D30360[d]	Cl	64	65	64	67	64	72	59	64	63	65		
	Br	30	35	36	32	36	28	41	36	37	35		
	I	6			1								
D31665	Cl	63	63	64	68	65	69	66	68	64	67		
	Br	37	36	36	30	35	31	34	32	33	33		
	I		1		2					3			
D36399[e]	Cl	67	67	68	73	63	65	63	65	71	62	68	64
	Br	33	33	32	27	37	35	36	35	29	38	32	36
	I							1					
D36399[f]	Cl				1	1		1					
	I	100	100	100	99	99	100	99	100	100	100		

D35996[g]	Cl	67	66	73	67	69	63	78	67	62	61	2	6
	Br	31	34	27	33	31	37	22	33	38	39		3
	I	2										98	91
D33111[h]	Cl	60	63	68	64	64	70	66	67	61	53	66	65
	Br	40	37	32	36	36	30	34	33	39	44	34	35
	I										3		
D32138[c]	Cl	56	79	80	73	57	85	81	64	77	55	56	60
	Br	42	21	15	27	42	15	19	32	23	45	43	40
	I	2		5		1			4			1	
D29066[i]	Cl	50	60	62	60	67	60	50	53	53	51	44	59
	Br	41	32	34	35	28	34	41	40	39	36	40	36
	I	9	8	4	5	5	6	9	7	8	13	16	5
D34495[c]	Cl	63	68	63	64	63	65	63	57	67	67	2	3
	Br	37	32	37	36	37	34	36	43	32	33	3	4
	I						1	1		1		95	93

[a] Analyses are reported in the same way as in Table 1. [b] Traces Fe, As detected. [c] Trace As detected. [d] Traces As, S, Fe detected. [e] Greenish yellow phase; traces Cu, As, Fe detected. [f] Bright yellow phase; traces Pb, As detected. [g] Traces Pb, As detected. [h] Traces Pb, As, Fe detected. [i] Trace Fe detected.

Table 5. Analytical data for miscellaneously attributed samples from Broken Hill, including the Broken Hill Consols Mine.[a]

No.		Analyses											
D46338[b]	Cl	60	57	57	53	56	57	58	68	56	66		
	Br	32	35	34	37	35	34	32	31	35	33		
	I	8	8	9	10	9	9	10	1	9	1		
D26168[c]	Cl	72	76	63	65	60	77	77	72	66	65		
	Br	28	24	37	35	40	22	23	28	34	35		
	I						1						
D28184[d]	Cl	75	68	86	70	70	70	78	70	84			
	Br	25	30	14	28	30	29	21	30	16			
	I		2		2		1	1					
D28185[d]	Cl	55	56	55	56	55	55	60	50	45	50	56	
	Br	43	43	44	43	44	43	40	46	45	45	41	
	I	2	1	1	1	1	2		4	10	5	3	

[a] Analyses reported as in Table 1. [b] Trace S detected. [c] Traces Pb, Cu, S, As detected. [d] Consols Mine; traces Pb, As, S, Fe detected.

Table 6. Silver halide analyses from deposits remote from the Broken Hill orebody.[a]

No.		Analyses											
D30482[b]	Cl	84	83	64	61	79	66	64	71	57	60	67	65
	Br	16	17	31	35	21	34	36	29	41	37	30	32
	I			5	4					2	3	3	3
D30480[c]	Cl	65	61	59	62	61	64	60	56	59	60		
	Br	30	35	36	34	35	31	36	39	37	35		
	I	5	4	5	4	4	5	4	5	4	5		
D30484	Cl	61	66	66	56	67	65	67	54	66	66	72	68
	Br	38	31	30	42	31	30	28	45	31	31	26	30
	I	1	3	4	2	2	5	5	1	3	3	2	2

D35460[d]	Cl	62	43	56	64	61	69						
	Br	38	53	43	36	36	31						
	I		4	1		3							
D28186[d]	Cl	59	59	72	64	67	64	66	62	67	65	66	68
	Br	40	41	28	33	29	33	32	38	31	32	32	30
	I	1			3	4	3	2		2	3	2	2
D18714[e]	Cl	74	71	66	79	71	77	75	72	70	70	76	73
	Br	26	29	34	21	29	23	25	28	30	29	24	27
	I										1		
D18719[f]	Cl	73	70	64	67	70	63	61	66	60	57	63	76
	Br	27	30	35	32	30	37	38	33	40	43	37	24
	I			1	1			1	1				
D18724[g]	Cl	67	67	63	67	65	63	67	61	71	65	73	61
	Br	33	33	37	33	35	37	33	39	29	35	27	39
D18712	Cl	76	78	85	76	62	84	82	75	85	76	68	66
	Br	24	22	15	24	38	16	18	25	15	24	32	34
D18720[h]	Cl	62	67	66	81	57	74	75	79	66	90		
	Br	38	33	34	19	43	26	23	21	34	10		
	I							2					
D18721	Cl	64	60	64	57	65	65	58	62	58	65	58	75
	Br	36	40	36	43	35	35	42	37	42	35	42	25
	I								1				

[a] Analyses reported in same way as in Table 1. [b] Traces Pb, As, P, Fe detected. [c] Traces Pb, S, Fe, As detected; see text re inclusions. [d] Traces Fe, As detected. [e] Trace of Pb detected. [f] Traces Pb, As detected. [g] Traces of Fe detected. [h] Traces P, As, Fe detected.

Table 7. Specimen descriptions for silver halides collected remote from the Broken Hill main lode.

D30482	LABEL: Model Republic Mine, Purnamoota, NSW. COMMENTS: Purple halide slug.
D30480	LABEL: Embolite (slug), Model Republic Mine, Broken Hill, NSW, Purnamoota. COMMENTS: Grey-purple halide slug with minor coatings of hematite and yellow iron oxyhydroxides.
D30484	LABEL: Model Republic Mine, Purnamoota, NSW. COMMENTS: Purple halide slug.
D35460	LABEL: Silverhalide weighing lbs, Caledonian Mine, Purnamoota, Broken Hill District, NSW. COMMENTS: Sawn mass of purple-grey halide containing patches of days and ferruginous gossan fragments.
D28186	LABEL: Cerargyrite in azurite, War Dance mine, Purnamoota, Barrier Ranges, NSW. COMMENTS: Block of azurite with vuglus containing azurite crystals some of which has altered to later malachite. The azurite is veined and coated in parts by later greenish grey halide.
D18714	LABEL: Embolite, Lily mine, Thackaringa, NSW. COMMENTS: Purple halide slug with minor copper straining and attached mica flakes on surface.
D18719	LABEL: Iodembolite with native silver, Bobby Burns Mine, Appolyon Velly, Barrier Range, NSW. COMMENTS: Sawn specimen of compact, ferruginous gossan containing large masses of green halide, some of which has been altered to native silver.
D18724	LABEL: Embolite with cerussite, Day Dream mine, Barrier Range, NSW. COMMENTS: Specimen matrix is massive, ferric oxyhydroxide-coated cerussite with rough, angular cavities containing green halide masses and infrequent malachite.
D18712	LABEL: Cerargyrite, Black Bird mine, near Silverton, NSW. COMMENTS: Vein in-fill of halide in decomposed sehist.
D18720	LABEL: Embolite, Maybell North, Mt. Gipps, Barrier Range, NSW. COMMENTS: Purple-brown, arborescent to massive halides in ferruginous clay matrix.
D18721	LABEL: Cerargyrite, Maybell North Mine, M. Gipps, Barrier Range, NSW. COMMENTS: Mass of grey-purple to green halide coated with minor clays and iron oxyhydroxides on a decomposed schist base.

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Graptolite Zonation in the late Wenlock (Early Silurian), with a New Graptolite-Brachiopod Fauna from New South Wales

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ABSTRACT. The Panuara Formation at Cobblers Creek near Orange, New South Wales, Australia has yielded a graptolite-brachiopod fauna assigned to the *sherrardae* sub-Biozone (late Wenlock: Early Silurian). The *sherrardae* sub-Biozone as defined here is equivalent to the *praedeubeli* sub-Biozone, and is the lowest part of the *ludensis* Biozone. The *ludensis* Biozone is reappraised following restudy of the type specimens of *Monograptus ludensis*, which are shown to exhibit growth stages from the *deubeli* to the *gerhardi* condition.

The graptolite fauna consists of *Gothograptus chainos* Lenz, *G. marsupium* Lenz, *Pristiograptus jaegeri* Holland, Rickards & Warren, *Pristiograptus dubius* (Suess), *Monograptus ludensis* (Murchison), *Monograptus moorsi* n.sp., *Monograptus* sp. and *Lobograptus sherrardae* (Sherwin). The limited shelly fauna includes the brachiopods *Plectodonta brownae* n.sp., *Bracteoleptaena pannucea* n.sp. and *?Lissatrypa*.

RICKARDS, R.B., & A.J. WRIGHT, 1997. Graptolite zonation in the late Wenlock (Early Silurian), with a new graptolite-brachiopod fauna from New South Wales. Records of the Australian Museum 49(3): 229–248.

Silurian strata in the vicinity of the New South Wales central western city of Orange have yielded important and abundant graptolite faunas (e.g., Sherrard, 1954; Packham & Stevens, 1955; Sherwin, 1971a, 1982; Jenkins, 1978, 1986; Rickards, Packham, Wright & Williamson, 1995) as well as abundant shelly fossils (see Pickett, 1982). The small but significant fauna of graptolites and shelly fossils, from Silurian exposures in Cobblers Creek, a tributary of Panuara Rivulet (Fig. 1) described here, was discovered by Ray Smith (1966) during mapping of the Mandurama-Panuara district, south of Mount Canobolus; the locality is about 30 km roughly SSW of Orange (Fig. 1). Our initial collections were made by Henry Moors, Norman Savage and Tony Wright in about 1963; further collections were made by Barrie Rickards, Penny Williamson and Wright in 1989, and again by Wright in 1996. The graptolites are described by Rickards, and the brachiopods by Wright; trilobite identifications are by Andrew Sandford of the Museum of Victoria, Melbourne, Australia.

Geological setting

On the Molong-Wellington High (Pickett, 1982), abundant shallow marine Silurian faunas occur in well known limestone sequences such as are developed in the Borenore, Cheesemans Creek, Quarry Creek and Four Mile Creek areas (Rickards *et al.*, 1995). Closely associated with these limestones are important graptolitic sequences; Rickards *et al.* (1995) summarised previous work on these Llandovery, to at least Ludlow, faunas.

During pioneering work in the region (Stevens, 1953), the Silurian strata yielding these Cobblers Creek and other graptolite faunas were named the Panuara Formation (see also Packham & Stevens [1955] and Smith [1966]). In the recent re-mapping of the Bathurst 1:250,000 sheet by the Geological Survey of NSW and the Australian Geological Survey Organisation (Pogson & Wyborn, 1994), the detailed stratigraphic terminology introduced by Jenkins (1978) for exposures in the Panuara area, some 3 km north of our Cobblers Creek locality, was followed. Rickards *et al.* (1995) noted some problems in the usage of this terminology, so we use the older lithostratigraphic name Panuara Formation here.

The fossils were collected from grey to tan shales and siltstones, and fine sands which are almost certainly distal turbidites. These beds dip at 62° degrees towards 328° in Cobblers Creek, at grid reference 799 891 on the Canowindra 8630-I & IV 1:50,000 topographic sheet. Hand-specimens often exhibit scale slumping and scouring, and consist mostly of interbedded brown, often bioturbated mudstone and fine greyish graptolitic or radiolarian siltstone to gritty sandstone. Some bedding planes are strewn with quartz grains and flakes of white mica up to about 1 mm in size. In order of abundance, the fauna consists of graptolites, radiolarians, "articulate" brachiopods, ostracodes, trilobites, and rare cystoid plates, phosphatic brachiopods and hyolithids.

Shelly material (almost invariably moulds) occurs rarely, scattered on bedding planes; one bedding surface exhibits an encrusting bottom fauna. Most of the shells are transported, separate valves, although conjoined valves of *Plectodonta* (in the "butterfly" configuration) do occur; some *Bracteoleptaena* valves are broken. Para-autochthonous moults of trilobites are rare; taxa identified by Andrew Sandford include ?*Latiproetus* and ?*Maurotarion*. The graptolites are often current-aligned and occur with or without other, less abundant but usually complete, macrofossils. Preservation of the graptolites is generally excellent, with periderm in all but weathered specimens; many are uncompressed. Most graptolites and brachiopods in the fauna are slightly tectonically deformed.

In terms of biogeography, the cosmopolitan Cobblers Creek brachiopod genera support the Old World connection previously indicated for the region (Rong *et al.*, 1995). The plankton-dominated fauna is clearly deepwater (at least outer shelf) and close to the limit of tolerance for the shelly benthos.

Biostratigraphic horizon of the Cobblers Creek graptolites

Smith (1966) assigned this graptolite fauna to the Melbournian stage, based on his identification of "Varieties of *Monograptus tumescens*". As discussed by Brown *et al.* (1968), the term Melbournian (Gregory, 1903) was broadly defined, but was later restricted to part of the Ludlow (Late Silurian, see VandenBerg *et al.*, 1976: 58); it is irrelevant here as it has been discarded in recent discussions of Victorian Silurian biostratigraphy (e.g., VandenBerg *et al.*, 1976; Rickards & Sandford, in press).

Our collections can be referred unequivocally to what has been called by most workers the *ludensis* Biozone of the late Wenlock (Early Silurian) (see Rickards, 1995; Koren' *et al.*, 1996); subdivision of this Biozone has been discussed by many authors (see Rickards *et al.*, 1995 for summary). The presence of *Lobograptus sherrardae* (Sherwin), especially those extreme variants which approach quite closely to *Pristiograptus idoneus* (Koren') (see section on Evolution) at Cobblers Creek, in association with *M. ludensis* ("*praedeubeli*" and *ludensis* growth stages), indicates a level low in the *ludensis* Biozone or in what we prefer to call the *sherrardae* sub-Biozone (see below). Equally, the absence of *M. deubeli*, recorded from the Quarry Creek district (Rickards *et al.*, 1995) some 20 km away, indirectly supports an early *ludensis* age for our fauna. *Gothograptus chainos* and *G. marsupium* were first described by Lenz (1993b) from the latest part of the *lundgreni-testis* Biozone in the Canadian Arctic but, at Cobblers Creek, these species occur with a distinct *ludensis* assemblage; these two species thus appear to range up into the *sherrardae* sub-Biozone, low in the *ludensis* Biozone.

The lowest part of the *ludensis* Biozone has been variously labelled by different authors: *praedeubeli* (Jaeger, 1991), *sherrardae* (*praedeubeli*) (Koren', 1992), *ludensis praedeubeli* (Lenz, 1993a) and *sherrardae praedeubeli* (Lenz, 1994b). It seems to us that the most sensible label for this assemblage biozone is the *sherrardae* sub-Biozone of the *ludensis* Biozone. This then avoids problems that may arise with respect to *M. praedeubeli* (see discussion under the *M. ludensis* problem).

Few Australian graptolite faunas can be compared with this assemblage; *ludensis* zone faunas are well known from Quarry Creek (Rickards *et al.*, 1995), but there is surprisingly little taxonomic similarity, and we conclude that our Cobblers Creek fauna is slightly older.

From the Forbes district of New South Wales, Sherwin (1975) described Silurian faunas belonging to the *sherrardae* sub-Biozone as do the Cobblers Creek fauna and, where taxa are similar, they are discussed in the taxonomic section. The association of "*dubius*"-type monograptids, *Lobograptus sherrardae* and retiolitids in the Forbes fauna is reminiscent of the fauna discussed here.

The emerging, updated account of the Silurian graptolites of Victoria (Rickards & Sandford, in press) offers excellent prospects for establishing correlations between New South Wales and Victoria on the basis of graptolite faunas. However, there is no clear equivalent of the Cobblers Creek

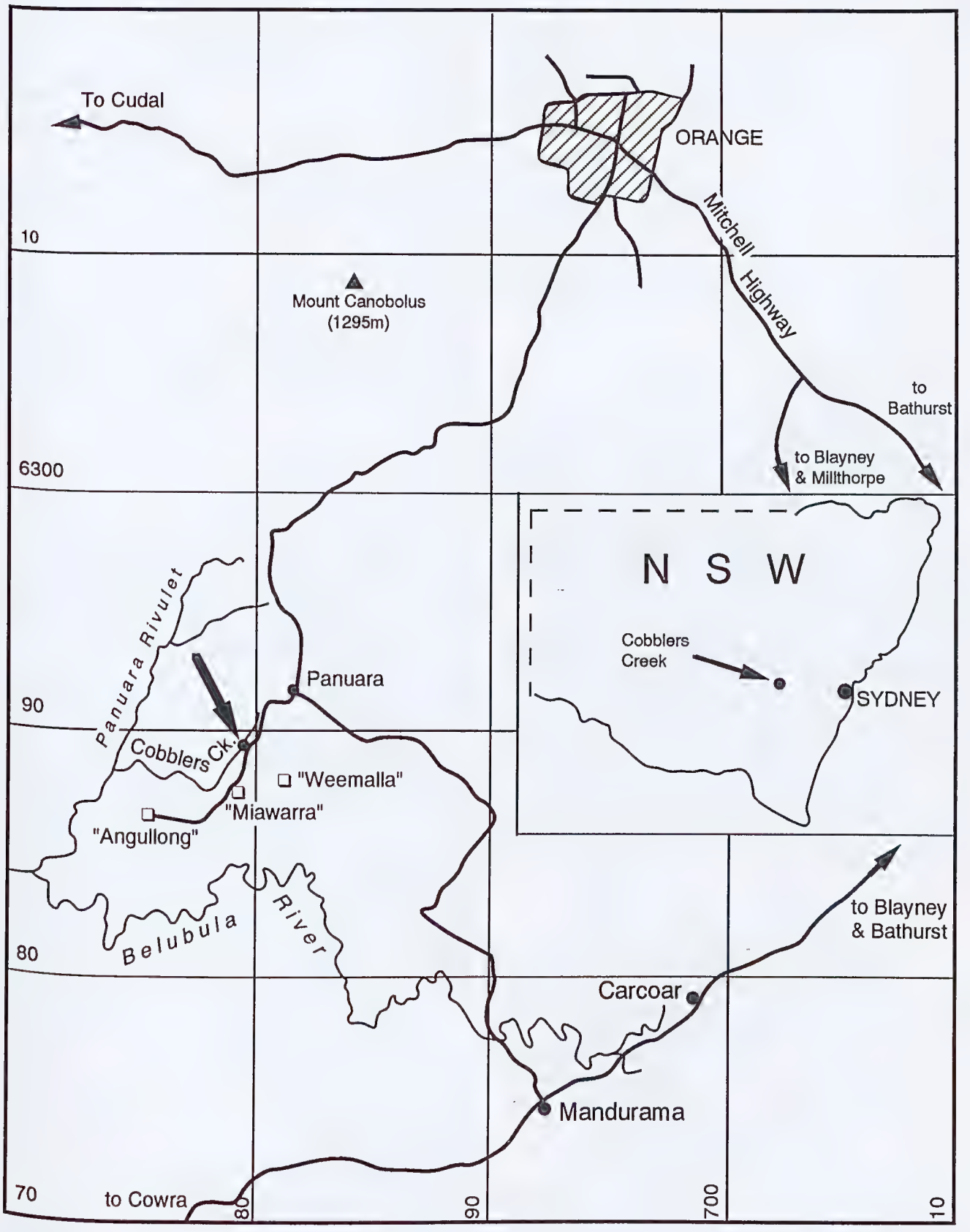

Fig. 1. Sketch topographic map for the Cobblers Creek locality; grid spacing 10 km.

fauna in Victoria. Garratt (1975) recognised and listed a probable *nassa* zone graptolite fauna from the Anderson Creek Formation in Victoria which included *Gothograptus nassa* (Holm), *Monograptus flemingii* Salter, *M.* cf. *ludensis* (Murchison) and *Pristiograptus* cf. *jaegeri* Holland, Rickards & Warren. Rickards & Sandford (in press) state that the formation has a suspected range of low Wenlock to high Wenlock (possibly including the very base of the *ludensis* Biozone), thus approximately confirming Garratt's age for the assemblage.

In the New South Wales context, the occurrence of shelly fossils with graptolites at Cobblers Creek provides more information on the local ranges of these Silurian shelly forms, as well as contributing to the solution of the problem that exists in differentiating Wenlock from Ludlow shelly faunas in Eastern Australia. The parlous state of knowledge reflected by the range chart given by Sherwin (in Pickett, 1982; fig. 10) listed 6 brachiopod taxa for the *lundgreni-testis* to *ludensis* interval; more recent data have been summarised by Strusz & Garratt (in press).

The occurrence in the Cobblers Creek fauna of *Plectodonta* extends the range of the genus well below the Přídolí range cited by Cocks & Rong (1989) for *Plectodonta bipartita* (Chapman), most species of the genus being Devonian. *Bracteoleptaena* has not been previously reported from Australia, although species assigned to the genus indicate generic ranges from Ashgill to Wenlock in Europe (Temple, 1965, 1968; Havlicek, 1967; Cocks, 1978); the late Wenlock age for the Cobblers Creek fauna does not conflict with this range. Other members of the shelly fauna (e.g., ?*Lissatrypa* sp. and the trilobites) are too tentatively known to be of stratigraphic value; species of *Lissatrypa* are known from the Llandovery at Heathcote, Victoria (Öpik, 1953) up to the Early Devonian (e.g., Philip, 1962: in the Boola Beds, Tyers, Victoria). From the Nandan facies of Guangxi, Xu Hankui (1977, 1979) described a Middle Devonian brachiopod fauna characterised by diminutive genera including notanopliids, but also two species of *Plectodonta* and an atrypid *Holynatrypa mirabilis*; the latter bears some gross resemblance to the form described below as ?*Lissatrypa*.

Evolution of Cobblers Creek graptolites

Koren' & Urbanek (1994) suggested a possible evolutionary origin of *Lobograptus sherrardae* from *Pristiograptus idoneus* (Koren'). We support this suggestion in that some of the straighter members of our collection of *L. sherrardae* are very close to *P. idoneus*, but differ in still having the rounding of th 1. Material described by Lenz (1995) must also be very close to this plexus but, as he rightly said, it is distinguishable from *P. idoneus* in having a lappetted th 1, and from *L. sherrardae* in its straight rhabdosome and small sicula.

It is clear from our record of *Monograptus moorsi* n.sp. and *Monograptus* sp. that there is more to resolve in the evolution of *Monograptus* s.st. at this stratigraphic level. At one time it was considered that the genus was absent from the *ludensis* Biozone, but it is clear that at least the *flemingii* group continues, rarely and locally (see Rickards *et al.*, 1995). *Monograptus moorsi* cannot be readily placed in any previously described species grouping, so elucidation of its evolution must await further records.

Pristiograptus jaegeri may be important in the early evolution of the *ludensis* group. *Pristiograptus dubius* (Suess) is usually considered the likely ancestor of the *ludensis* group (Rickards *et al.*, 1977; Koren' & Urbanek, 1994); however, recent work suggests that there is some difficulty in distinguishing *P. jaegeri* from *M. praedeubeli* Jaeger, 1991 (but see section on the *ludensis* problem below). For example, some (perhaps all) material referred by Lenz (1994c) to *M. praedeubeli* is unquestionably referable to *P. jaegeri*. The latter species has only occasionally a rounded aperture to th 1, and the derivation of *M. ludensis*, including its early growth stage (*M. "praedeubeli"*), from *P. jaegeri* requires that this feature became dominant and that the sicula curved ventrally instead of being quite straight. Little else is needed. Thus it is possible that *M. ludensis* evolved only indirectly from *P. dubius* via the morphologically and stratigraphically intermediate species *P. jaegeri*.

The *Monograptus ludensis* Problem

Some controversy has continued over the taxonomy of the *ludensis* species group (Jaeger, 1991; Rickards *et al.*, 1995) ever since Holland *et al.* (1969) first revised the group. We have taken the opportunity raised by our Cobblers Creek records of *M. ludensis* to re-examine the type series of the species (British Geological Survey Museum number 6584), originally figured by Murchison (1839, plate 26, fig. 2 [*non* fig. 1]); the specimen BGSM 6584a was selected as holotype by Holland *et al.* (1969).

There are at least 80 current-oriented specimens of a monotypic assemblage on the type slab (BGSM 6584) and another slab (BGSM 6582). Preservation is in full relief and there is no tectonic deformation of the sandy nodule from which the two pieces were derived. Holland *et al.* (1969) figured only their selected lectotype from the type series, but further preparation by us has revealed further rhabdosomes with excellently-preserved proximal ends which are figured herein (Figs 4A–C,E).

The first point to recognise is that Figs 4A–E represent a growth series, and that each step in that series is represented by numerous specimens. Earlier growth stages (Fig. 4A) are narrower and have less thecal overlap, although the thecal spacing remains the same and th 1 is distinctly rounded. This is the form which equates with *Monograptus praedeubeli* Jaeger in some recent papers (Jaeger, 1990, 1991; Koren', 1992; Lenz, 1995). Later growth stages show that the thecal tubes continue to grow and that there is a tendency, visible even as early as Fig. 4B, for the ventral thecal lip to grow more distally than ventrally—to change direction, in fact. Figure 4B conforms approximately to *M. vulgaris* Wood, 1900 (which Holland *et al.* [1969] placed in synonymy with *M. ludensis*) and Figs 4C–D approach the change to what has been described as *M. gerhardi* Kühne (see Kühne, 1955; Jaeger, 1991;

Gutiérrez-Marco *et al.*, 1996). In short, the syntype series of *M. ludensis* embraces several "species" increasingly being used to characterise subdivisions of the old *M. ludensis* Biozone (see, for example, Koren', 1992; Rickards *et al.*, 1995). Fortunately, these subdivisions of the *ludensis* Biozone do not depend solely upon *M. praedeubeli* and *M. gerhardi* and, whatever the taxonomic complexities of the *M. ludensis* group, the current three subdivisions of the *ludensis* Biozone seem quite workable (see Rickards *et al.*, 1995: fig. 4; Rickards, 1995: fig. 5).

Two further matters arise from our revision of the types. The first concerns the growth stage potential in differing depositional realms. There is some suggestion that records of this species group from shelf deposits, such as in Shropshire (U.K.) and parts of central Europe and the Canadian Arctic, conform fairly closely to Jaeger's concept of *M. praedeubeli*, whereas contemporaneous down-slope, offshore deposits, such as are seen in Wales and the Lake district, yield the full growth series as seen on the type slab of *M. ludensis*. Thus, the Much Wenlock Limestone Formation of the Ludlow district (Holland *et al.*, 1969) yields *M. ludensis* close to the *M. praedeubeli* stage, whereas deposits of the same age in Wales and the Lake district yield this form as well as all growth stages up to and including *M. gerhardi*. In contrast, Lenz (1994b, 1994c, 1995) did not record *M. gerhardi*. Furthermore, these down-slope deposits yield very large and long specimens, well over 2 mm broad and up to 140 mm long, not seen in shelf occurrences of the species group.

The second matter concerns the supposed biostratigraphic value of *M. praedeubeli, M. ludensis* and *M. gerhardi*. The three forms are supposed to follow each other in time, with *praedeubeli* first, then *ludensis*, and finally *gerhardi* (possibly reaching into the *nilssoni* Biozone), but with considerable overlap between them. This might work if only individual shelf sequences are considered but, if offshore, deeper-water deposits are considered (as in the case of the type collections of *M. ludensis*), it is immediately clear that *M. praedeubeli* is an early growth stage of, and technically a junior synonym of, *M. ludensis*. One compromise on this issue, suggested provisionally by Rickards *et al.* (1995), was that three subspecies (*ludensis praedeubeli, l. ludensis* and *l. gerhardi)* be recognised until the palaeogeography and precise correlation were more refined, when the question can be reassessed, including the possibility of ecophenotypic variation. Our preferred subzonal scheme for this *ludensis* Biozone is threefold: *sherrardae*, followed by *deubeli* and *gerhardi* (highest). Justifications of the two major changes are that the first name avoids problems generated by the *praedeubeli-ludensis* relationship and the second name permits retention of the long-ranging *ludensis* for the higher level biozone.

Monograptus gerhardi is a rather different matter from *M. praedeubeli* in this context because it does seem, on current evidence, that the stratigraphically later forms of the *ludensis* group do reach the *gerhardi* condition more commonly. The procedural suggestion by Rickards *et al.* (1995) does at least have the merit of recording the growth stages identified in any particular section. Future work will then gradually test whether these taxa are stratigraphically viable forms or not. For example, the current distinction in some papers, such as Lenz (1994b,c, 1995), of a *praedeubeli* Biozone overlain by a *ludensis* Biozone is suspect. Note that in Lenz (1994b, 1994c, 1995) the ranges of the recorded *praedeubeli* and *ludensis* in particular sections are more or less the same, with the former appearing slightly earlier in some sections, and the latter appearing slightly earlier in others; *M. gerhardi* was not recorded.

The relationship between *P. jaegeri* and *M. praedeubeli* is discussed here in the section on evolution, but is relevant in that the very earliest records of *M. praedeubeli* recorded by Lenz (1995) may be close to the origin of the latter from *P. jaegeri*, and the full *M. ludensis* range of growth may not have been developed. That is admittedly speculative, and for future work to examine; but *M. praedeubeli* of Lenz (1995) is here referred to *M. ludensis*.

Systematic palaeontology

Type material is deposited at the Australian Museum, Sydney (AMF), the British Geological Survey Museum, and at the Museum of Victoria, Melbourne (NMV). A selection of comparative material is lodged in the Sedgwick Museum, Cambridge.

In this section, no new terms are proposed. The calculation of thecal spacing follows the method of Packham (1962) in which measurements for 1–3 thecae are extrapolated to give thecae per millimetre. This, we maintain, gives a more clear indication of thecal spacing changes along the rhabdosome than other methods and, in particular, gives a figure more easily compared with traditional measurement (which counts the number of thecae per unit length) than does the method of Howe (1983). The diagnoses given refer to the Cobblers Creek material, and are not a synthetic species abstract. Comparisons of Cobblers Creek biocharacters are made, as appropriate, with type and other material. Cobblers Creek material is deformed by a cleavage at a high angle to the bedding. In the descriptions corrections are made for this, unless otherwise indicated.

Class Graptolithina Bronn, 1849

Note that the date for Bronn's first mention of the class has been commonly given as 1846; our research shows that the date of publication was 1849.

Order Graptoloidea Lapworth, 1873

Family Plectograptidae Boucek & Münch, 1952

Subfamily Gothograptinae Obut & Zaslavskaya, 1986

Gothograptus Frech, 1897

Type species. *Retiolites nassa* Holm, 1890; Late Wenlock *nassa* Zone, Eske Beds, Gotland, Sweden; by original designation.

Gothograptus chainos Lenz, 1993b

Figs 5A–B

1993b *Gothograptus chainos,* new species; 17–18, pl. 7, figs 1–12.
1994a *Gothograptus chainos* Lenz, 1993b; Lenz, 858, pl. 5.1–8

Material examined. Numerous fragmentary specimens. Figured specimens AMF 81782 and NMV 146877.

Diagnosis. Small gothograptid up to 5 mm long and 0.70–0.90 mm wide, comprising only clathrial elements. Corona bowl-shaped, rounded. Thecal apertures alternating, 10 in 10 mm. Apertural regions thickened in some specimens, but no thecal hoods. Nema free, at least for most of rhabdosomal length. Clathrial meshwork of subpolygonal spaces, occasionally square or rounded; usually 4 sets of meshes, arranged in linear fashion, on the free "wall" of each theca.

Remarks. Although not so well preserved, these specimens closely resemble those illustrated by Lenz (1993b) in all dimensions and overall appearance. It is the dominant retiolitid at the locality, most rock fragments having a few complete or fragmentary specimens. It differs from the other retiolitid in the assemblage, the more robust *G. marsupium*, which is described below. The latter species certainly reaches a dorso-ventral width of 2.0 mm, has an ovate rather than parallel-sided rhabdosome, and has inwardly-sloping "supra-genicular" walls; in all of these features it differs from *G. chainos*.

Gothograptus marsupium Lenz, 1993b

Fig. 5C

1993b *Gothograptus marsupium*, new species; Lenz, 18–19, pl. 10, figs 1–9; pl. 11, figs 1–8.
1994d *Gothograptus* n.sp.; Lenz, pl. 4, figs B,F,G.
1995 *Gothograptus* sp.; Rickards *et al.*, 41, figs 18K–L, 20J.

Material. Figured specimen AMF 92265, and some possible fragments.

Diagnosis. Gothograptid with rhabdosome up to 3 mm long and 2 mm broad, with conspicuous thecae outlined by clathrial elements; "supragenicular" wall inward-sloping, no "genicular" hood present; thecal spacing 11–13 in 10 mm; rhabdosome narrows a little distally; virgula present; all clathrial elements fine, providing a squarish meshwork, interspersed with even finer reticular threads.

Remarks. Although fragmentary, our specimens are identical in structure and dimensions to the originals of Lenz (1993b), except that the pouch-like thecal profiles are not so clear. Rickards *et al.* (1995) misleadingly described the thecae of *Gothograptus* as "strongly keeled" when they were, in fact, referring to the "supragenicular" walls and geniculum. Those Quarry Creek specimens are from the *ludensis* Biozone, as is the material described here from Cobblers Creek. Lenz (1993b) recorded *G. marsupium* from the *lundgreni-testis* level, but in New South Wales the species occurs in the *ludensis* Biozone.

Pristiograptus Jaekel, 1889

Type species. *Pristiograptus frequens* Jaekel, 1889; Ludlow, glacial drift boulders, North Germany; by original designation.

Pristiograptus jaegeri Holland, Rickards & Warren, 1969

Figs 2A–B, 5F–I

pars 1900 *Monograptus vulgaris* Wood, 455–6, text-fig. 10a (non 10b, pl. 256, fig. 2).
non 1900 *Monograptus vulgaris* var. b Wood, 457, pl. 25, fig. 3.
non 1911 *Monograptus vulgaris* var. *curtus* Elles & Wood, 379, pl. 37, fig. 11.
pars 1911 *Monograptus vulgaris* Wood; Elles & Wood, 378–379, text-fig. 248a (non 248b, pl. 37, fig. 2).
?1935a *Monograptus vulgaris* Wood; Decker, 443–444, figs 32–4.
?1935b *Monograptus vulgaris* Wood; Decker, 309.
?pars 1944 *Pristiograptus vulgaris vulgaris* (Wood); Příbyl, text-fig. 2L (non 2M), 22–23.
?1947 *Monograptus vulgaris* Wood; Ruedemann, 490, pl. 84, figs 22–24.
?1948 *Pristiograptus* cf. *vulgaris vulgaris* (Wood, 1900); Příbyl, 78.
non 1960 *Monograptus vulgaris* var. *ashlandensis* Berry, 1163, fig. 2H.
1963 *Monograptus vulgaris* Wood; Holland, Lawson & Walmsley, 104, 136, 157.
1969 *Pristiograptus jaegeri* n.sp.; Holland, Rickards & Warren, 668–671; pl. 130, fig. 1; text-figs 2k–r, 3f.
1974 *Monograptus (Pristiograptus)* aff. *jaegeri* Holland, Rickards & Warren; Cuerda, 328–330; pl. 3, figs 1–8; pl. 4, figs 1–4.
1975 *Pristiograptus jaegeri* Holland, Rickards & Warren; Berry & Murphy, 71–73; text-fig. 21a; pl. 8, fig. 3.
1994b *Pristiograptus dubius dubius* (Suess); Lenz, 1420, figs 2A–D.
pars 1994b "*Pristiograptus*" *praedeubeli* (Jaeger); Lenz, 1420, figs 2E–G, 3A–E.
1995 *Pristiograptus jaegeri* Holland, Rickards & Warren, 1969; Rickards *et al.*, 41–2, figs 22F–G, 24A–G.

Material. AMF 81780, 81792, 92253–4, 92267 and NMV 146878; the material is variously deformed, some specimens being little deformed, some in low relief.

Diagnosis. *Pristiograptus* with straight rhabdosome, including the proximal end, up to 30 mm long. Proximal dorso-ventral width 0.65–0.70 mm, gradually reaching 1.30–1.50 mm more distally. Proximal thecal spacing about 15 in 10 mm, and distally as low as 10 in 10 mm. Thecal overlap 1/2 proximally, changing to 2/3 distally.

Description. The above diagnostic figures are corrected for tectonic deformation. Thecal spacing, for example,

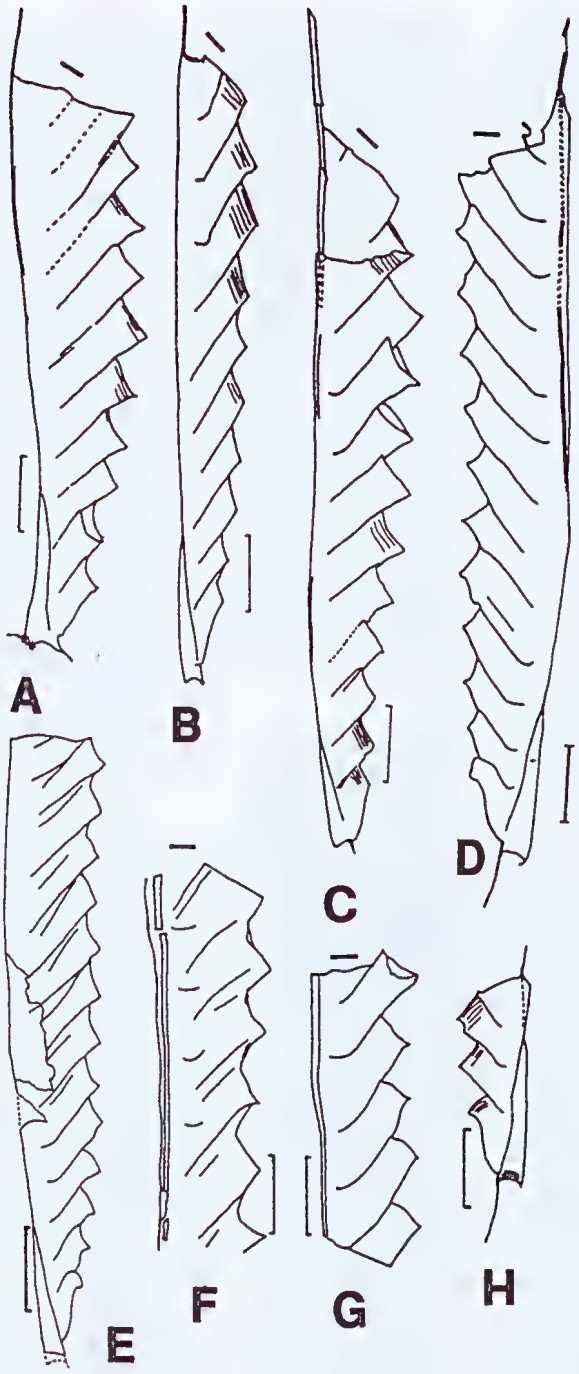

Fig. 2. **A–B**, *Pristiograptus jaegeri* Holland *et al.*, 1969; respectively AMF 92253–4, showing the effect of tectonic deformation on dorso-ventral width and thecal overlap in extreme cases (A). **C**, *Pristiograptus dubius* (Suess), NMV 146884. **D–H**, *Monograptus ludensis* (Murchison), respectively AMF AMF 92255–6, AMF 92258–60. Lineation caused by tectonic deformation shown by short heavy bar; scale bars 1 mm, all approximately ×10.

varies from 13 in 10 mm to 19 in 10 mm at the proximal end, but specimens at 45° to the lineation have 15–16 in 10 mm. The sicular length is also affected but, in undeformed specimens or when corrected, is 2 mm long; its apex reaches to just above the aperture of th 2. The proximal end is quite straight in almost all specimens; even those specimens normal to the lineation show no increase in rhabdosomal curvature. The first theca shows a very slight rounding of the aperture in a small number of specimens.

Remarks. The thecal spacing is slightly higher than in the type series described by Holland *et al.* (1969) from Shropshire and Wales, the latter ranging from 12–8 in 10 mm. However, all other measurements are the same and the overall aspect, especially the straight proximal end, are identical. The Cobblers Creek specimens are very similar to the Quarry Creek material (Rickards *et al.*, 1995).

Jaeger (1991) considered one specimen of the type series (Holland *et al.*, 1969, text-fig. 2m) of *P. jaegeri* a synonym of *M. praedeubeli* Jaeger but, as pointed out by Rickards *et al.* (1995), this is unlikely because **most** specimens in an assemblage of *M. praedeubeli* have a rounded aperture to th 1, whereas in the type series of *P. jaegeri* rounding of th 1 is rare. Furthermore, it should be pointed out that *P. jaegeri* has priority over *M. praedeubeli*.

Jaeger (1991: 327) was also of the opinion that, based on an examination of three specimens of *P. jaegeri*, that it was a junior synonym of *P. dubius*. This is certainly wrong, as is well exemplified by the Cobblers Creek collection of at least 100 specimens; all are quite straight proximally with no sign of the characteristic slight ventral curvature of *P. dubius*. Comparison of Figs 2A–B and 2 C shows the differences between our recorded specimens of *P. jaegeri* (which are abundant) and *P. dubius* which are quite rare at Cobblers Creek. In addition to the question of curvature of the rhabdosome, the sicula is longer and differently positioned in *P. jaegeri*.

The species figured by Lenz (1994b) from the Canadian Arctic as *"Pristiograptus" praedeubeli* (Jaeger) seems to us to be classical *P. jaegeri* in that there is little or no rounding of the aperture of th 1. Furthermore, the other dimensions resemble the type material closely, more closely even than our Cobblers Creek material.

These problems of identification highlight the rapid evolutionary diversions taking place in the *ludensis* Biozone, especially amongst this species group. The global range of *P. jaegeri* (see Holland *et al.*, 1969) is late *lundgreni* to *nilssoni* Biozones, although it is rare in the latter biozone.

An evolutionary origin of *M. praedeubeli* (= *M. ludensis praedeubeli* of Rickards *et al.*, 1995) from *P. jaegeri* at the base of the *ludensis* Biozone seems very likely.

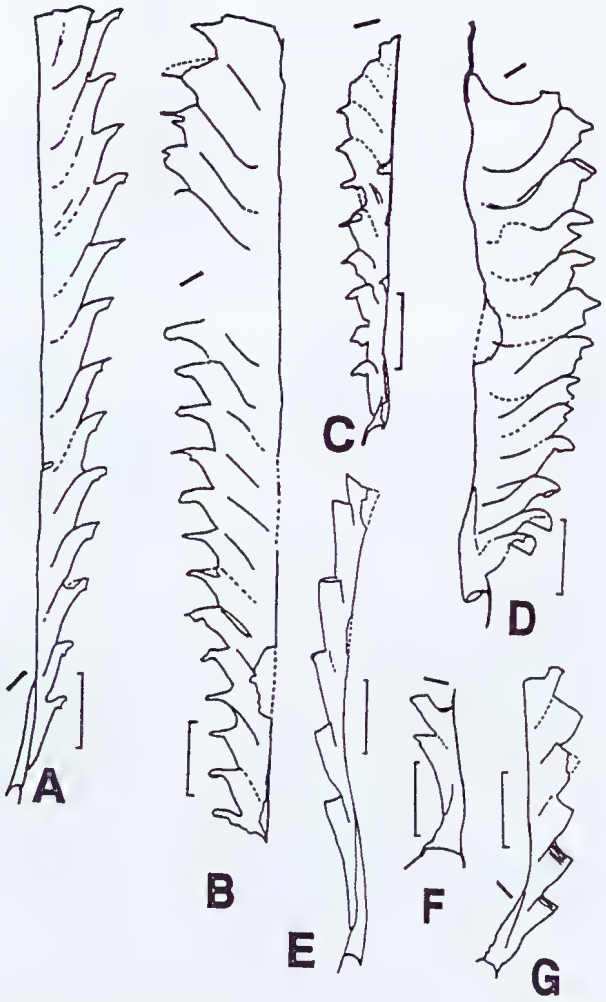

Fig. 3. **A–C**, *Monograptus moorsi* n.sp., respectively AMF 92261 (holotype), AMF 92262–3. **D**, *Monograptus* sp., AMF 92264. **E–G**, *Lobograptus sherrardae* (Sherwin), respectively NMV 146883, NMV 146875 and NMV 146882. Lineation caused by tectonic deformation shown by short heavy bar; scale bars 1 mm, all approximately ×10.

Pristiograptus dubius (Suess, 1851)

Figs 2C, 5D–E

1851 *Graptolithus dubius* Suess: 115, pl. 9, figs 5a,b.

Material. AMF 81781, 92266.

Remarks. This species has been discussed briefly above; it occurs very rarely in the fauna.

Monograptus Geinitz, 1852

Type species. *Lomatoceras priodon* Bronn, 1835; Étage E, Bohemia; designated by Bassler (1915).

Monograptus ludensis (Murchison, 1839)

Figs 2D–H, 4A–E, 5J

1839 *Graptolithus ludensis* Murchison, 694, pl. 26, fig. 2 (*non* fig. 1); for a full synonymy, see Rickards *et al.* (1995).

1990 *Monograptus praedeubeli* n.sp.; Barca & Jaeger, figs 11/11–12.

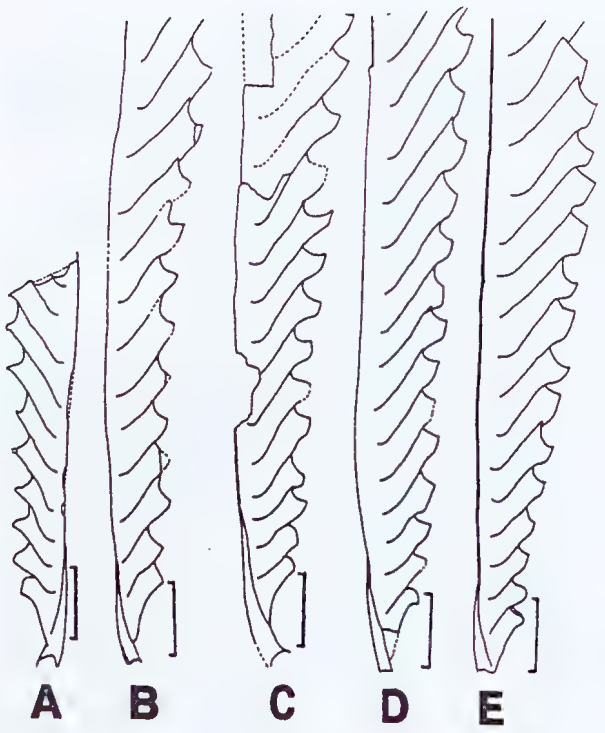

Fig. 4. A–E, *Monograptus ludensis* (Murchison), a growth series selected from Murchison's type slab, British Geological Survey Museum no. 6582/4; **A**, "*praedeubeli*" growth stage; **B**, same, but with some further growth of thecae and slightly distal turning of the free ventral wall (incipient "*gerhardi*" stage, essentially the *ludensis* or *vulgaris* growth stage); **C**, further growth stage showing increased dorso-ventral width, length of thecae, and further development of *gerhardi* condition; **D**, lectotype 6584a, with moderately advanced "*gerhardi*" condition; **E**, an example of the most robust specimens on the slab, which may reach 50 mm in length; all specimens tectonised, in full relief; scale bars 1 mm, approximately ×10.

1995 *Colonograptus? ludensis* (Murchison); Lenz, 1385, figs 9D–I, 11N,O,W,X.

1995 *Colonograptus? praedeubeli* (Jaeger); Lenz, 1385–6, figs 9P–R, 11A–D.

1996 *Colonograptus ludensis* (Murchison, 1839); Lenz *et al.*: 1396, figs 3P,Q, 4M–R.

Material. Numerous well-preserved specimens, being only second in abundance to *P. jaegeri* (see above section entitled "The *Monograptus ludensis* problem"). Figured specimens are: AMF 81791, 92255–6, 92258–60; several specimens from the type slab BGSM 6582/4, including the lectotype 6582a.

Description. The Cobblers Creek specimens have a rounded th 1, occasionally th 2 to some extent, and exhibit only the *praedeubeli* and *ludensis* growth stages (see discussion above on *ludensis* problem). Sicular length 1.80–2.40 mm; apex usually about the level of the aperture of th2. The dorso-ventral stipe width reaches 1.30–1.50 mm, and the thecal spacing is 13–11 in 10 mm. The thecal apertural regions are sometimes slightly concave just below the apertural lip.

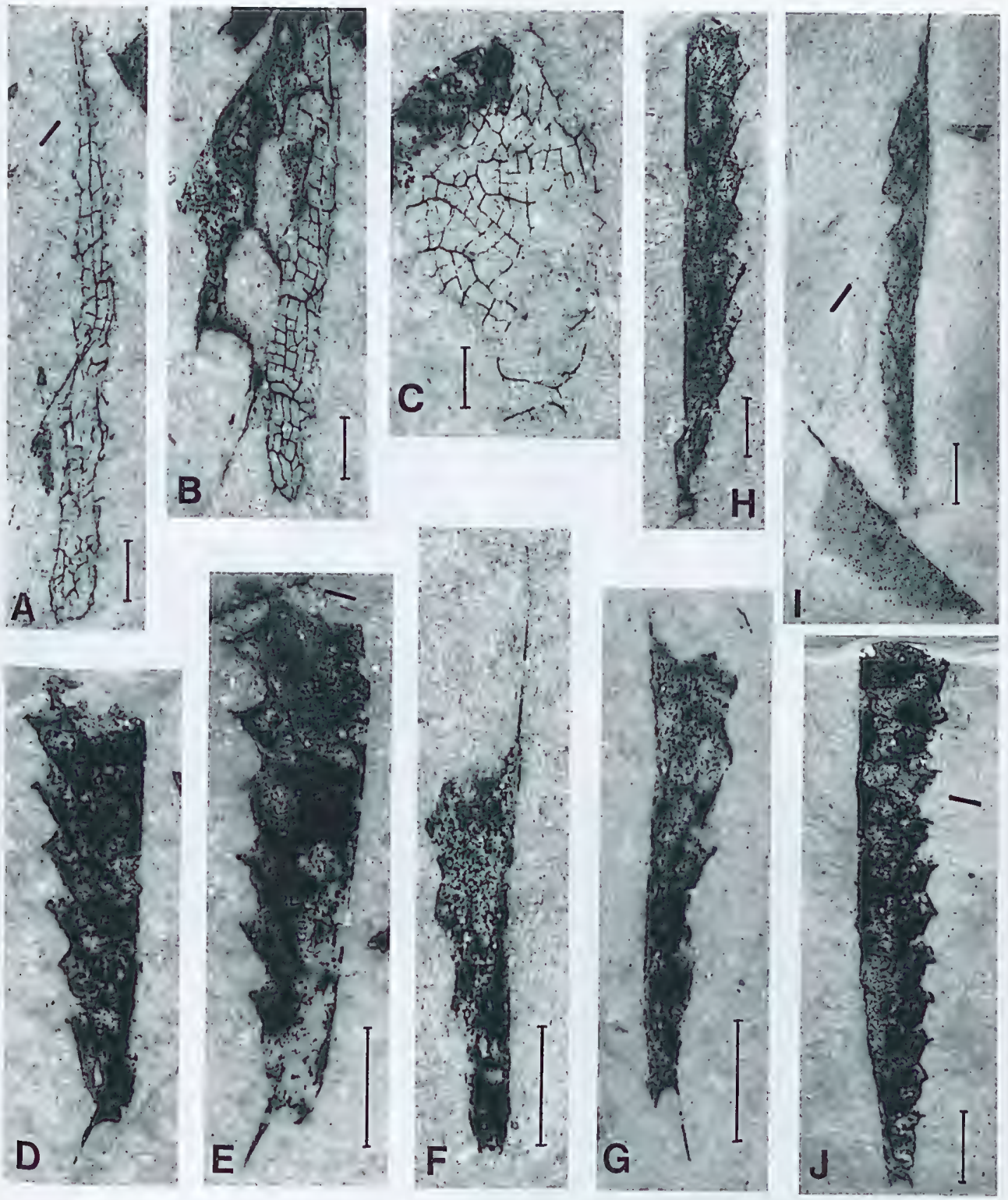

Fig. 5. **A–B**, *Gothograptus chainos* Lenz, respectively NMV 146877 and AMF 81782, profile and subapertural views. **C**, *Gothograptus marsupium* Lenz, AMF 92265. **D–E**, *Pristiograptus dubius* (Suess), respectively AMF 92266 and AMF 81781. **F–I**, *Pristiograptus jaegeri* Holland *et al.*, 1969, respectively AMF 81792, AMF 92267, NMV 146878 and AMF 81780; **I**, shows the extreme tectonic deformation seen on some surfaces. **J**, *Monograptus ludensis* (Murchison), AMF 81791. Lineation caused by tectonic deformation shown by short heavy bar; scale bars 1 mm, all approximately ×10.

Remarks. A diagnosis for this species was given by Rickards *et al.* (1995). The relationship of *M. ludensis* to *M. praedeubeli*, *M. vulgaris* Wood, *M. gerhardi* and *P. jaegeri* is discussed above in the sections on the *ludensis* problem and on the evolution of some Cobblers Creek graptolites. The latter specimens closely resemble the type series of Murchison and differ only in that they show a slight concavity just below the apertural lip.

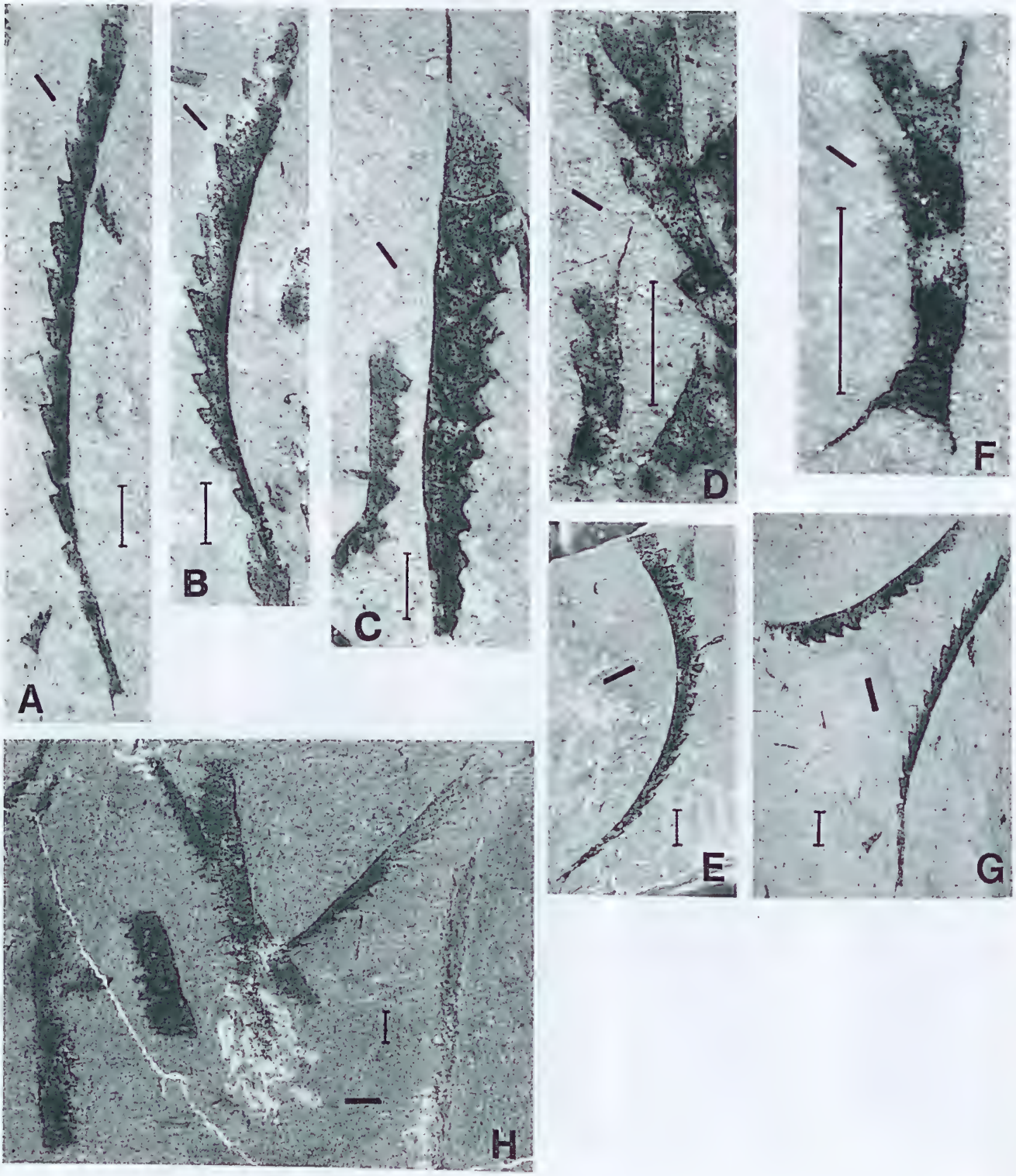

Fig. 6. A–G, *Lobograptus sherrardae* (Sherwin); **A**, NMV 146879, with typical proximal end somewhat attenuated by stretching; **B**, NMV 146880, more distal thecae; **C**, NMV 146881, proximal end made more robust by stretching, associated with specimen of *P. dubius* (Suess); **D**, NMV 146885, proximal end showing curved sicula, nema, together with a fragment of distal thecae; **E**, NMV 146886, specimen with increased curvature as a result of stretching; **F**, NMV 146876, showing characteristically curved sicula with flared sicular aperture, and completion of th 2 before growth of th 3; **G**, NMV 146799, relative deformation of two adjacent specimens. **H**, *Monograptus moorsi* n.sp., holotype AMF 92261 (diagonal specimen; see also Fig. 3A) associated with AMF 92262 (central upright specimen; see also Fig. 3B) and other fragmentary specimens of the same species. Direction of tectonic stretching indicated by short bar; scale bar 1 mm.

Monograptus moorsi n.sp.

Figs 3A–C, 6H

Material. HOLOTYPE AMF 92261; figured PARATYPES AMF 92262–3 and other specimens are known with certainty only on the same slab as the holotype.

Derivation of name. The species is named for Dr Henry Moors, in recognition of his work on Australian graptolites.

Diagnosis. Almost straight *Monograptus*, at least 10 mm long; distal dorso-ventral width up to 1.30 mm, gradually expanding from a proximal dorso-ventral width of 0.40 mm. Thecal spacing about 16–17 in 10 mm proximally, 14 in 10 mm distally. Thecal overlap about 1/2 proximally, 2/3 distally. Thecal hook occupies almost 1/2 rhabdosomal width proximally, and as little as 1/4 distally. Hook pronounced, but without strong retroversion. Sicula about 1.30 mm long, reaching to above level of the hook of th 1.

Description. The rhabdosome is more or less straight at the proximal end, the sicula providing a conspicuous dorsal addition (Fig. 3A). The virgella is thickened and robust in one specimen (Fig. 3C) but is fine and straight in others (e.g., Fig. 3A). Its apex is seen a little way along the hook of th 1. Proximal thecal hooks suggest more retroversion more than distal hooks and they occupy a greater proportion of the rhabdosomal width. As the thecal overlap increases distally, so the ratio of thecal hook to stipe width falls. The nature of the thecal hooks is uncertain. It seems that both dorsal and ventral walls are involved in the hooks but, on the more distal thecae, the most distal part of each hook has a curiously flattened appearance. This may indicate the presence of paired lappets on distal thecae, rather than dorsal wall retroversion.

Remarks. *Monograptus moorsi* is distinct from the *flemingii* group as the hooks are different, lacking the clear retroversion and thecal spinosity, and in having narrow, straight proximal ends with a sicular apex positioned more proximally. *Monograptus moorsi* differs from *M.* ex. gr. *flemingii* recorded from the *ludensis* Biozone at Quarry Creek (Rickards *et al.*, 1995) in having a higher thecal spacing (16–14 in 10 mm compared with 12–10 in 10 mm) as well as on the general grounds just stated. Thus *M. moorsi* represents a new record of *Monograptus* s.s. for the *ludensis* Biozone, as only forms of the *M. flemingii* group have been previously recorded (see Rickards *et al.*, 1995: 9).

Monograptus moorsi differs from *M. uncinatus* Tullberg in having a less retroverted hook and a much higher thecal spacing, whereas the proximal end in *M. uncinatus* tends to have a slight ventral curvature and is more robust.

Monograptus insperatus Koren', which occurs in the *ludensis* Biozone of Peshkaut, Kirghizia and the same horizon in Victoria (see Rickards & Sandford, in press), has paired thecal lappets and is more robust, with a ventrally curved sicula. The thecal spacing of *M. moorsi* is about twice that of *M. insperatus*.

Monograptus sp.

Fig. 3D

Material. A single specimen, AMF 92264 a, b.

Description. The rhabdosome is 6 mm long, and has a maximum dorso-ventral width of 1.50 mm achieved at a length of 3 mm. However, the specimen is clearly tectonically deformed, as indicated not only by the lineation on the bedding surface but also by the undulating dorsal margin and nema. The sicula is 1.50 mm long, slightly curved ventrally, although this curvature is exaggerated by deformation. Thecal overlap is considerable, being at least 1/2 proximally and 3/4 distally. The thecae are clearly hooked, but the nature of the hook is obscure. The first two thecae appear to have the dorsal margin strongly retroverted, and there is a clear indication of this in the most distal thecae. Other thecae suggest that the ventral margin is also retroverted; in other words, the thecal hook is of *priodon* style. However, there is a slight suggestion that on thecae 5–9 lappets may be present, although this may be an artefact of preservation. In brief, the thecae are strongly hooked but the nature of the hook cannot yet be ascertained. Thecal spacing (deformed) is 20 in 10 mm, suggesting (allowing for deformation of the specimen) an original spacing of about 16 in 10 mm.

Remarks. The overall appearance and measurements are similar to *Monograptus banksi* Rickards *et al.*, 1995, but the latter is more robust and has a strongly curved sicula. *Monograptus dalejensis dalejensis* of Rickards *et al.*, 1995 is similarly distinct from *M.* sp. It is possible that *M.* sp. is related to the *M. flemingii* group, and may be the proximal end of the *M.* ex gr. *flemingii* described by Rickards *et al.* (1995) from the *ludensis* Biozone at Quarry Creek, but the deformation of *M.* sp. does not allow us to be certain about this. Another possible comparison is with *M. insperatus* from the *ludensis* Biozone of Peshkaut, Kirghizia. The same species has been recorded from Victoria (Rickards & Sandford, in press). The thecal spacing in *M. insperatus* is much less than in *M.* sp. and the two are similar only in overall dimensions and rhabdosomal shape.

For the moment it is clearly advisable to leave the Cobblers Creek specimen in open nomenclature, whilst noting that it is yet another record from the *ludensis* Biozone as the evolutionary diversity increases after the *nassa/dubius* evolutionary low point.

Lobograptus Urbanek, 1958

Type species. *Monograptus scanicus* Tullberg, 1883; Cardiolaskiffern (Ludlow), Marianelund, Scania, Sweden; by original designation.

Lobograptus sherrardae (Sherwin, 1974)

Figs 3E–G, 6A–G

1971b	*Monograptus* spp. D, E; Sherwin, 167–171, pl. 17, figs 2,5,7.
1974	*Pristiograptus sherrardae* n.sp.; Sherwin, 231, pl. 2, figs 1–10, text–fig. 3a–e.
1978	*Pristiograptus etheringtoni* n.sp.; Lenz, 635, pl. 2, figs B–F, text-figs 1.4–6.
1980	*Monograptus*? aff. *deubeli* Jaeger; Lenz, 635, pl. 6, figs 1,3.
1988	*Monograptus sherrardae* Sherwin; Koren' & Rinenburg, 12, pl. 1, figs 13–15,18.
1992	*Lobograptus? sherrardae* (Sherwin, 1974); Koren'; 31–32, pl. 3, figs 4–5; pl. 4, figs 3–6.
?1994c	*Lobograptus? sherrardae* (Sherwin); Lenz, 1780, figs 3a, 4a–c.
1994c	*Lobograptus*? aff. *sherrardae* (Sherwin); Lenz, 1780–1, figs 3b–h, 4d–f, 4m–n.
1995	*Lobograptus? angustus* n.sp.; Lenz, 1387–1388, figs 10A,B, 11T–V.

Material. The ten figured specimens are NMV 146875–6, 146879–83, 146885–7.

Diagnosis. *Lobograptus* with dorsally curved rhabdosome; curvature gentle to moderate, except at the extreme proximal end where the ventrally curved sicula imparts a ventral curvature to the rhabdosome as a whole. Sicular apex near or just above th 1 aperture; sicular aperture flared, with conspicuous virgella; sicular length approximately 2 mm; th 1 apertures slightly rounded in profile as a result of lateral lappets; thecal overlap 1/3 proximally, 1/2 distally; all thecae subsequent to th 1 have pristiograptid apertures. Distal dorso-ventral width 0.75 mm. Thecal spacing about 12 in 10 mm distally, and 15 in 10 mm proximally.

Remarks. The Cobblers Creek specimens are identical to Sherwin's original material from the Forbes district, N.S.W., except that the thecal spacing may be slightly higher (12–15 compared to 11–14). However, there is clearly some variation when global records are considered. For example, Koren' (1992) cited 9–13 in 10 mm, and Lenz (1994b) 11–13 in 10 mm proximally. Lenz's (1994b) specimens appear to be rather more robust proximally than Sherwin's or our material; indeed, his specimens described as *L.*? aff. *sherrardae* seem closer to the N.S.W specimens. *L.*? aff. *sherrardae sensu* Lenz (1994b) seem to show some tendencies towards *L.*? *claudiae* Koren', although it lacks the thecal apertural isolation of *L.*? *claudiae*; Lenz later named his Canadian form *L.*? *angustus*. Clearly there is some variation in this species group, and possibly some of that variation may prove to be valuable stratigraphically.

Phylum Brachiopoda

Class Strophomenata Williams *et al.*, 1996

Order Strophomenida Öpik, 1934

Family Plectambonitacea Jones, 1928

Plectodonta Kozlowski, 1929

Type species. *Plectodonta mariae* Kozlowski, 1929, from the Borschov Horizon, Mitkov Beds (Prídolí), Podolia, Ukraine (Cocks & Rong, 1989); by original designation.

Remarks. The oldest species accepted by Cocks & Rong (1989) in *Plectodonta* is the Ludlow-Prídolí *Plectodonta thuringica* Schmidt, 1939; thus it is important to note the Wenlock age of the species described here, and that *P. bipartita* (Chapman, 1913) occurs (as *P. davidi* Mitchell, 1923) in the Rainbow Hill Marl Member (Ludlow) in the Yass district of New South Wales, immediately above the occurrence of *Bohemograptus*. Several of the Silurian species assigned to *Plectodonta* by Havlicek (1967) and Cocks & Rong (1989) are Australian. The Devonian occurrence of the genus in Australia is well documented (e.g., Philip, 1962).

Plectodonta brownae n.sp.

Figs 7A–O, ?8A–C

Material. HOLOTYPE: conjoined valves AMF 99584a–h. PARATYPES: conjoined valves AMF 99614, 99587; brachial valves AMF 99586, AMF 99589, NMV 146098; pedicle valves AMF 99591–3, AMF 99594–5, AMF 99615–6; NMV 146100.

Derivation of name. For the late Dr Ida Alison Browne (née Brown), in recognition of her contribution to understanding of middle Palaeozoic geology of New South Wales (e.g., Brown, 1941; Browne, 1959; Brown & Sherrard, 1952).

Diagnosis. *Plectodonta* with resupinate brachial valve, internally characterised by several short radial ridges posterolateral of the main septa (especially in smaller shells), and numerous low and rare large papillae. Sculpture parvicostellate, with up to about 15 primary ribs separated by 4–5 secondary costellae; up to 7.3 mm wide and 4.2 mm long.

Description. Transversely semi-oval, concavo-convex shells; resupinate brachial valve initially gently convex, becoming gently concave, pedicle valve convex throughout. Hingeline straight, and weakly denticulate for less than half shell width. Parvicostellate sculpture, with up to about 15 primary ribs separated by 4–5 secondary costellae, and often impressed internally; primary ribs appear by intercalation. Maximum width 7.3 mm, maximum length 4.2 mm.

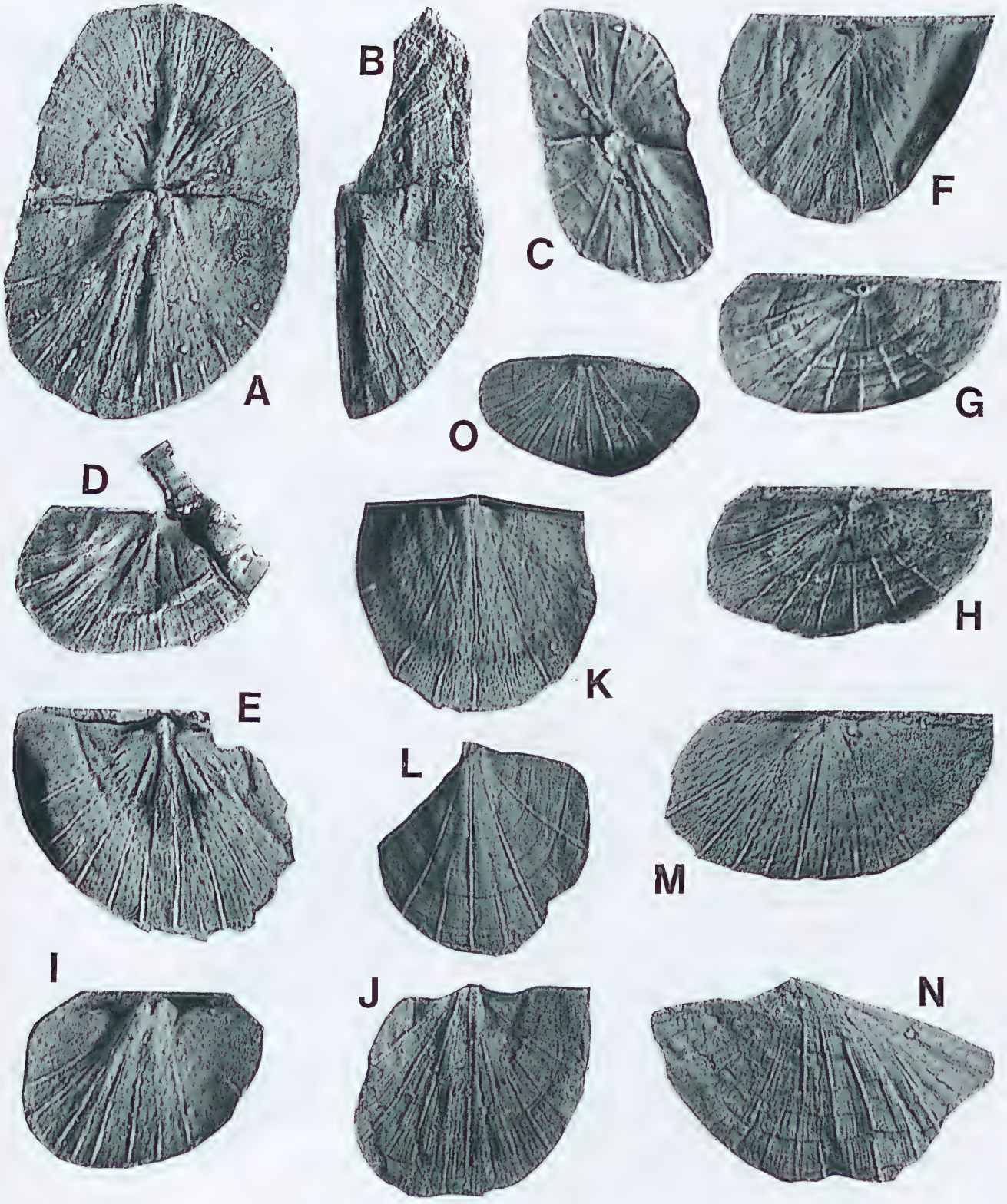

Fig. 7. A–O, *Plectodonta brownae* n.sp. **A–B**, AMF 99584, holotype brachial internal and latex cast of external surfaces, ×10; **C–O**, all paratypes, all internal moulds unless otherwise stated: **C**, AMF 99587, conjoined valves, ×20; **D**, AMF 99614, brachial valve, with incomplete pedicle detached, ×12; **E**, NMV 146098, brachial valve, ×10; **F**, AMF 99586, brachial valve, ×10; **G–H**, AMF 99588, brachial valve and external cast, ×12; **I**, AMF 99592, pedicle valve, ×12; **J**, AMF 99591, external cast, pedicle valve, ×12; **K–L**, AMF 99593, pedicle valve and external cast, ×10; **M**, AMF 99594, pedicle valve, ×10; **N**, AMF 99615, external pedicle cast, ×12; **O**, AMF 99616, external pedicle cast, ×12.

Brachial interior finely papillate; external radial sculpture strongly impressed, especially near margin. Muscle field slightly elevated; adductor scars large and flabellate in mature specimens, with lobes separated by prominent radial ridges of varied lengths; medially short, with faint ridge anteriorly. Narrow medial groove arises in pit at front of essentially bilobed cardinal process, and becomes weaker anteriorly. Sockets low and set at high angle to hingeline, with low rounded socket ridges. The two major septa are gently convex outwards from just in front of cardinalia, diverging from medial line at about 20°, to just past mid-length and, beyond the "lophophore platform", are almost straight for anterior half of length where they are located just medially of the traces of the first costellae lateral to the medial costella. Each major septum is flanked and parallelled by one, or rarely more, almost straight secondary septa set at about 60° to the hingeline, and reaching to about half the length of the longer septa; in one specimen, the space between the major and secondary septa is occupied by a short ridge. These are, in turn, flanked posterolaterally by about 4–5 smaller radial ridges described above; posteromedial part of lophophore platform finely papillate.

Pedicle valve also bears widespread imprint of external sculpture, but is more papillate than brachial valve. Muscle scars divided posteriorly by short, narrow myophragm, anterior of which the muscle field bifurcates; adductor scars not clearly differentiated. Delthyrium apparently open, teeth stout.

Remarks. The brachial valves exhibit what Philip (1962) called the "lophophore platform", which lacks papillae.

The small plectambonitaceans (whose dimensions, given above, must be used with discretion as all specimens are deformed) in this collection fall into three groups:

i The majority of the material is assigned to *P. brownae* n.sp. This species differs from *P. bipartita* (Chapman, 1913) in size and the number of primary ribs, as well as the accessory brachial septa. It also lacks the coarse papillae seen outside the brachial muscle field of both *P. bipartita* and *P. mariae*. Another species from New South Wales, described as *Stropheodonta davidi* by Mitchell (1923: pl. xli, figs 19–21), was re-illustrated by Brown (1948: pl. XIV, figs 1–4) and assigned to *Plectodonta*. Savage (1974) suggested that the species is a junior synonym of *P. bipartita*.

ii. Four specimens (AMF 99585, 99588, 99590, NMV 146099) in the collection lack secondary costellae, but are assigned to *Plectodonta* sp. (Figs 8D–G) as denticulation has been observed along the hinge line of this sparse material. Fine, almost linear features between the primary costellae (as in Figs 8E–G) are caused by parallel clay particles. Only further material can establish the relationships of this form to *P. brownae*.

iii. Two further parvicostellate specimens have a relatively large number of primary costellae (NMV 146101–2, Figs 8A–C) for their valve size. They are here assigned tentatively to *P. brownae*, as they exhibit about 15 costellae at a width of 4.8 mm (NMV 146101) and ca 12 costellae at width of 4.7 mm (NMV 146102).

Comparisons. Other comparable Australian forms include: "*Plectodonta* n.sp." of Talent (1965), which lacks the parvicostellate sculpture of *P. brownae* n.sp.; and *P. bipartita* from the Late Silurian of the Melbourne district (Talent, 1965). Both *P. bipartita* and *P. davidi* lack the accessory septa which characterise the brachial valve of *P. brownae*. *Sowerbyella*? *plebia* Talent, 1965 from Heathcote, Victoria (assigned by Cocks & Rong to *Plectodonta*) appears to lack both a denticulate hingeline and the characteristic brachial septa. Both Philip (1962) and Savage (1974) figured specimens with a prominent marginal zone, showing prominent papillae and impression of sculpture, lacking in *P. brownae*, on the interior of valves of *Plectodonta bipartita*.

Mitchell (1923) described a number of new species of small plectambonitaceans from the Yass district of New South Wales, including *Stropheodonta davidi, Stropheodonta minuta, Stropheodonta tarloensis* and *Stropheodonta striato-costata*. Savage (1974) considered the first and last of these taxa to be synonyms of *P. bipartita*; material examined (AMF 27218, 28745, 28748) is parvicostellate (with 22–25 primary costellae) and has a gently sulcate brachial valve. The status and, indeed, the original location and stratigraphic horizons of Mitchell's other species is somewhat obscure. *Stropheodonta tarloensis* Mitchell does not appear to be a plectodontid. *Stropheodonta minuta* Mitchell is coarsely ribbed, and quite unlike *pannucea*. *Stropheodonta davidi* Mitchell appears to develop a bema in large specimens; this feature would exclude it from *Plectodonta*. Mitchell's (1923: 472, pl. 42, fig. 31) figured pedicle valve of *Stropheodonta striatopunctata* was described as having very numerous radials including fine striae, "numerous fine punctures on the very mildly convex valve, with a short slit-like septum"; this form is indeterminate.

Another similar species assigned to *Plectodonta* by Cocks & Rong (1989) is *P. sanglangensis* Xian (in Xian & Jiang, 1978: Eifelian; Guizhou province, China). This tiny species (about 4.5 mm wide and 2.5 mm long: Xian, 1978, pl. 97, figs 2,3) exhibits 7 primary costellae and lacks the small posterior septa characteristic of *P. brownae*, as do other species of *Plectodonta* listed by Cocks & Rong (1989).

Plectodonta sp.

Figs 8D–G

Material. AMF 99585, 99588, 99590; NMV 146099.

Remarks. The listed specimens lack secondary costellae, have a small dimple-like protegulal node on the subsequently concave brachial valve, and appear to lack the extra short, irregular brachial septa outside the normal two. As preservation is excellent, the lack of secondary costellae does not seem to result from adverse preservation; otherwise they are indistinguishable from *P. brownae*. This material is referred to *Plectodonta* as it shows a denticulate hinge line and paired brachial septa.

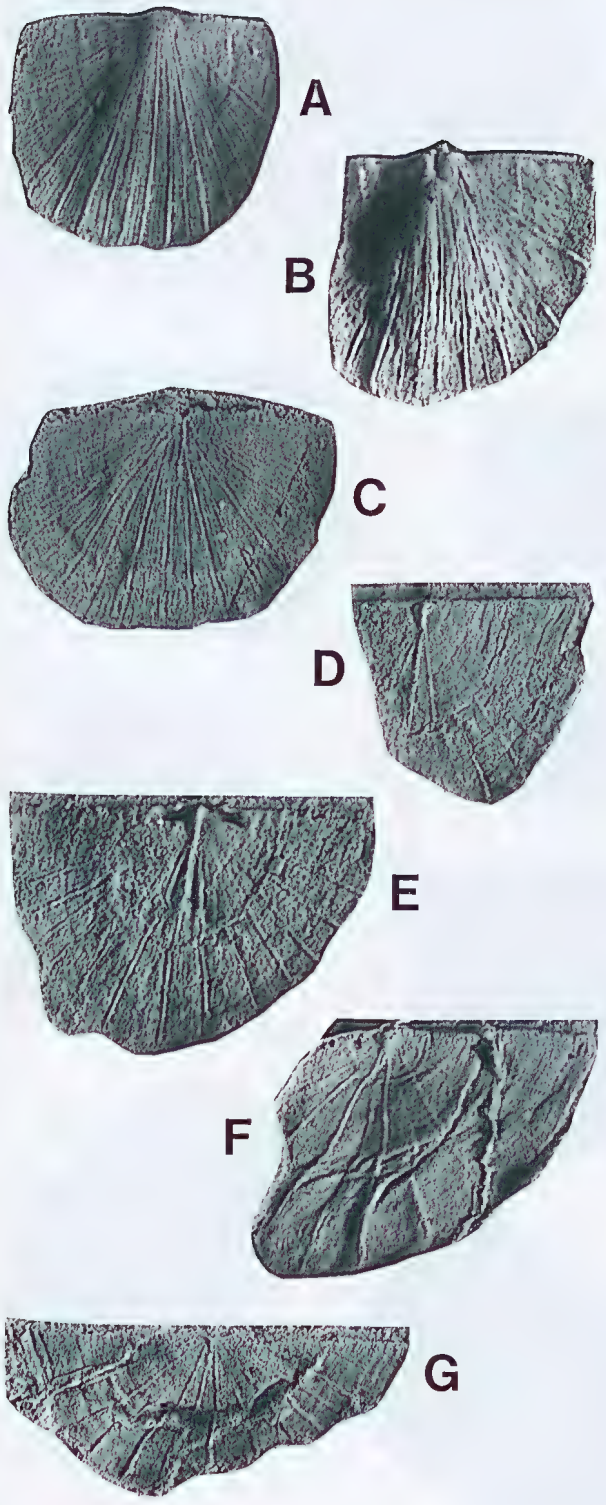

Fig. 8. A–C, *Plectodonta brownae*? **A–B**, NMV 146101, pedicle internal mould and latex cast of external surface, both ×10; **C**, NMV 146102, latex cast of pedicle valve, ×10. D–G, *Plectodonta* sp. **D–E**, AMF 99585, latex cast of external surface of brachial valve, and brachial internal mould, both ×10; **F**, latex cast of external surface of pedicle valve, AMF 99590, ×10; **G**, latex cast of external surface of pedicle valve, NMV 146099, ×8.

Family Ellipsostrophiidae Havlicek, 1967

Bracteoleptaena Havlicek, 1963

Type species. *Strophomena bracteola* Barrande, 1879, from the Wenlock Liten Formation, Borek near Suchomasty, Czech Republic; by original designation.

Remarks. Our species is clearly very close to the type species of *Bracteoleptaena* which, when erected, included the type species; subsequently, *Platymena polonica* Temple, 1965 was assigned to the genus by Temple (1968) and Cocks (1978). The latter species was chosen as type species of *Paromalomena* Rong. According to Chang (1981) this genus was established in 1979; however, Dr L. R. M. Cocks (pers. comm.) has kindly informed me that the name appeared in Rong (1979) only in a faunal list and a caption to an illustration and was, therefore, a *nomen nudum*. The genus was eventually formalised by Rong (1984).

Bracteoleptaena pannucea **n.sp.**

Figs 9A–K

Material. HOLOTYPE AMF 99603 a–b; PARATYPES AMF 92269, 99604–99612, 99631–3, ?99613.

Derivation of name. *Pannuceus* (L.), meaning wrinkled.

Diagnosis. *Bracteoleptaena* with plano-convex, non-sulcate shell, costellae poorly developed to lacking posterolaterally; weak dorsally-directed trail on mature pedicle valves. Dental lamellae short, sockets small and widely spaced; papillae in brachial valve restricted to outer part of adductor field.

Description. Shell very gently plano-convex with no sulcus, tongue or apophragm; elongate to transverse semi-oval in outline, with short alae. Both valves with an initial convex portion, but almost flat thereafter; mature pedicle valve weakly flexed dorsally at margins. Brachial interarea steeply hypercline, pedicle interarea steeply apsacline; both interareas flat and low. Width up to 15 mm, length about 8 mm. Radial sculpture ranges from absent, to weak, low costellae (posterolateral regions smooth); well-defined protegulal node, growth lines and weak rugae on both valves.

Brachial interior with slender socket ridges at less than 45° to the hingeline, and an elongate adductor field consisting of two elevated, elongate-oval scars divided by a slender medial furrow over most of length and a shallow depression posteriorly. Cardinalia crudely bilobed. Papillae on outer parts of adductor field, but sparse outside that region.

Pedicle valve dominated by the deeply conical, anteriorly-shallowing muscle field which reaches to about 1/3 of valve length; narrow, well-developed, slightly raised, elongate-oval central adductor field reaches to about anterior end of muscle field; larger diductor scars, showing prominent growth lines, are mostly located on flanks of muscle pit and bounded

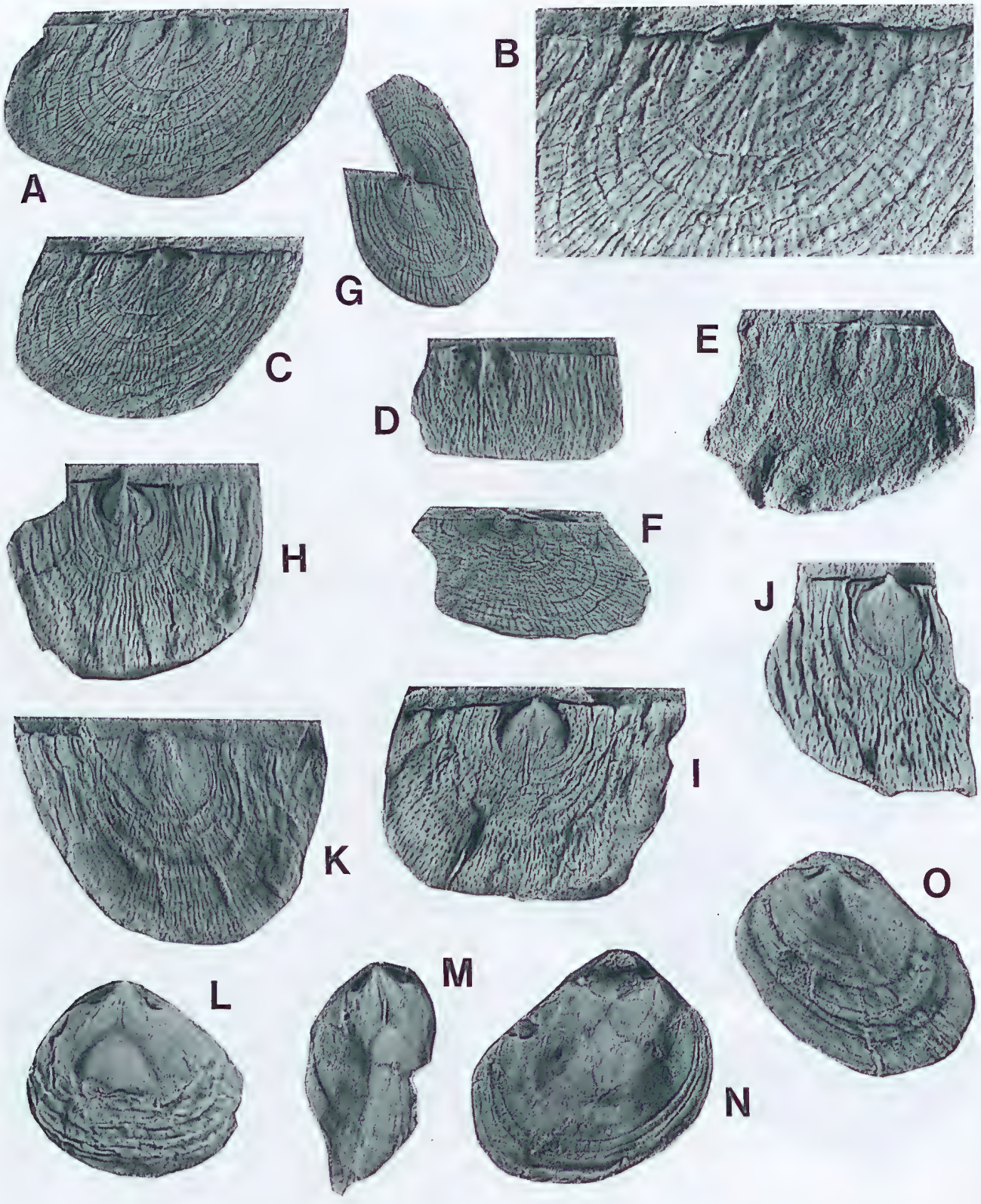

Fig. 9. A–K, *Bracteoleptaena pannucea* n.sp. A–C, AMF 99603, holotype brachial valve; **A**, internal mould ×5; **B**, posteromedial portion of A, showing sockets and weak, papillate muscle-bounding ridges, ×10; **C**, latex cast of external surface, ×5; D–J, paratypes: **D**, AMF 99607, brachial internal mould demonstrating elevated adductor muscle scars, and bounding furrows, ×6; **E**, AMF 99605, latex cast of brachial internal showing socket plates and elevated muscle scars, ×5; **F**, AMF 99604, external cast of brachial valve, ×6; **G**, AMF 99632, external cast of displaced pair of valves, ×5; **H**, AMF 99606, pedicle internal mould, ×5; **I**, AMF 99608, pedicle internal mould, ×4; **J**, AMF 99629, pedicle internal mould, ×6; **K**, AMF 99631, latex cast of pedicle exterior, ×5. L–O, *Lissatrypa*? sp. **L–N**, pedicle internal moulds, all ×6; **L**, AMF 99596, **M**, AMF 99599, **N**, AMF 99598; **O**, AMF 99600, brachial internal mould, possibly of this species, ×6.

laterally by low ridges which curve medially at anterior end of lobate scars. Short dental lamellae diverge at 45° to hingeline. Open delthyrium encloses apical angle of about 90°, possible foramen.

Remarks. This species assigned to the Ellipsostrophiidae rather than the Leptaenidae as it lacks the characteristic apophragm (Kelly, 1967) of the latter family. Much of our material seems to have undergone soft-sediment compaction, suggesting a thin, fragile shell which fractured due to sediment loading.

Previously described representatives of the genus are from Europe (Ashgill-Wenlock: Cocks, 1978) and China (Fu, 1975; Fu, 1982; Chang, 1981).

Comparisons. *Platymena polonica*, assigned by Temple (1968) and Cocks (1978) to *Bracteoleptaena*, has long, thin dental plates set at a higher angle to the hingeline than our material; this species has also been recorded from Dabashan Mountain, in the Yangtze Gorge region, China (Fu, 1975: 113) and Hubei (Chang 1981). Fu (1982: 123, pl. 35, figs 23,24) referred this species to *Paromalomena* Rong, 1984, in descriptions of faunas from northwest China. Chang (1981: 562) described *P. polonica* (pl. 1, fig. 29) and *P. hubeiensis* Chang (pl. 1, figs 34–36) from the Ashgill *Hirnantia* fauna of Hubei Province.

Bracteoleptaena pannucea differs from *B. bracteola* (Barrande, 1879) in lacking an anterior trail, in having less well-developed rugae, and having better developed muscle-bounding ridges in the pedicle valve. The less well known *B. degenera* Havlicek, 1967 is distinguished from *B. pannucea* by its prominent trail and partly parvicostellate sculpture.

Order Spiriferida Waagen, 1883

Superfamily Atrypacea Gill, 1871

Family Lissatrypidae Twenhofel, 1914

Lissatrypa Twenhofel, 1914

Type species. *Lissatrypa atheroidea* Twenhofel, 1914, from the Llandovery of Anticosti Island; by original designation.

?*Lissatrypa* sp.

Figs 9L–O

Material. AMF 99596–99 (pedicle valves), AMF 99600–1 (brachial valves).

Remarks. Pedicle valves in our collections display the characteristics of this vexatious genus (see Strusz, 1982). Important Australian species ascribed to this genus include *Lissatrypa tyro* (Öpik, 1953) and *L. lenticulata* Philip, 1962. The only reasonably preserved brachial valve in the collections may not be conspecific with the pedicle valves, as it has a dorsal sulcus and more "atrypid" cardinalia (Fig. 9M). *Lissatrypa lenticulata* differs from *L. tyro* in having a stronger "shoe-lifter" process in the pedicle valve, and a more massive hinge plate; both species have a sulcate pedicle valve.

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The Amphipod (Crustacea) Stygofauna of Australia: Description of New Taxa (Melitidae, Neoniphargidae, Paramelitidae), and a Synopsis of Known Species

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Abstract. Freshwater amphipods from Australian subterranean waters are discussed. Five new genera and fourteen new species are described; the genus *Wesniphargus* Williams & Barnard is rediagnosed and specimens assigned to *W. nichollsi* (Straškraba) are fully described; a synopsis of subterranean species is provided.

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Introduction

The diversity of Australian sub-surface (stygobiont) amphipods was, until recently, considered to be relatively low; only four or possibly five species were regarded as subterranean (Williams, 1986). However, in a separate footnote to the paper by Williams (1986: 556), Knott foreshadowed greater diversity and noted that a range of undescribed subterranean amphipods occurred in Western Australia. Without formal description of taxa, comments supporting this note were separately published (Knott, 1983, 1985). Descriptions of several subterranean species (Williams & Barnard, 1988; Stock & Iliffe, 1991; Barnard & Williams, 1995; Bradbury & Williams, 1995, 1996a,b, 1997) have provided substantive confirmation that a diversity of forms occur, a phenomenon which includes—as elsewhere—both troglobitic and troglophilic forms (i.e. obligate and facultative sub-surface forms). Bradbury & Williams (1997) discussed and drew attention to this diversity, listed all described sub-surface forms, and noted the occurrence of several further undescribed taxa.

The main aim of the present paper is to describe the further taxa referred to by Bradbury & Williams (1997). Given their number and diversity, the opportunity is taken to update the synopsis of described forms and discuss them briefly. The opportunity is also taken to revise the generic description of *Wesniphargus* Williams & Barnard, 1988, in the light of additional material of *W. nichollsi* collected from a stream flowing from a cave and from a temporary pool.

Although the taxa described herein significantly increase the already considerable known diversity of subterranean Australian amphipods, still further new taxa await description; material is in our possession or known to us which points to the likelihood of new stygobiont taxa from Queensland (*Chillagoe* sp.), New South Wales, South Australia (northwestern, east-central, and southeastern), Tasmania, and Western Australia (Barrow Island, Varanus Island, Ashburton River, Nullarbor Plain). However, given the pressing need to focus attention on surface forms of Australian amphipods, rather than provide an exhaustive study of sub-surface forms, this material will form the basis of a subsequent paper.

While the major aim of this paper is taxonomic, we recognise—together with an increasing number of others (see especially: Christiansen, 1992; Culver *et al.*, 1995; Holsinger, 1994a,b; Kane & Culver, 1992)—that cave faunas, amphipods in particular, are of considerable scientific interest beyond their taxonomy, but that taxonomic studies like ours nevertheless continue to dominate studies of cave faunas. Notwithstanding this recognition, given the only recent knowledge of the extensive diversity of sub-surface amphipods in Australia and its still indeterminate limits, we believe taxonomic studies essential prerequisites at this stage.

Methods of dissection and description

These follow Bradbury & Williams (1996a).

The notation **M**, with an appended number, indicates the position of an object as a fraction of the distance from the base to the apex of an appendage; **S**, large robust seta; **s**, small robust seta. Abbreviations used in the figures are as follows: **A**, antenna; **Abd**, abdomen; **acc**, accessory; **C**, coxa; **d**, dorsal; **dact**, dactylus; **E**, epimeron; **fl**, flake; **flag**, flagellum; **g**, gill; **G**, gnathopod; **Hd**, head; **i**, inner; **juv**, juvenile; **L**, left; **lac**, lacinia mobilis; **lat**, lateral; **LL**, lower lip; **MD**, mandible; **med**, medial; **mol**, molar; **MP**, maxilliped; **MX**, maxilla; **O**, oostegite; **opp**, opposite; **p**, palp; **P**, peraeopod; **pl**, plate; **Pp**, pleopod; **R**, right; **st**, sternal gill; **T**, telson; **U**, uropod; **UL**, upper lip; **UR**, urosome; **1, 2, 3 ...7**, first, second, third ...seventh article, segment, somite or epimeron (as appropriate).

Mandibular palp setae are described using the notation of Karaman (1969) and Barnard & Barnard (1983). Lowry & Stoddart (1993) proposed a modified notation which removed many discrepancies, but as the former notation was developed for freshwater crangonyctoids it has not been necessary to employ the more detailed ones of Lowry & Stoddard (1993).

Melitidae Bousfield, 1973

Norcapensis n.gen.

Type species. *Norcapensis mandibulis* n.sp.

Diagnosis. Pleonite six with two small dorsolateral robust setae, rostrum obsolescent, lateral cephalic lobes strongly projecting, broad, no antennal sinus, eyes absent. First antenna: elongate, longer than second antenna, ratio of peduncular articles 34:31:12, accessory flagellum 2-articulate, second article tiny. Second antenna: very short, flagellum much shorter than peduncle, calceoli absent. Upper lip: symmetrical, ovate. Mandible: palp three-articulate, articles reduced with few setae; accessory blades (rakers) on mandibles few with two plumose setae anteriorly; few small setae beyond rakers on to base of molar. Lower lip: with inner lobes. Maxillae: moderately to well setose medially; inner plate of first maxilla ovate with medial and distal plumose setae; outer plate with seven or more denticulate robust setae, palps symmetric, each with thin apical robust setae. Inner plate of second maxilla with row of plumose medial setae extending to the apex, some facial; both plates of second maxilla with plumose apical setae of medium to moderate length. Inner plate of first maxilla and medial and lateral margins of second poorly pubescent. Maxilliped: inner plate long with distofacial row of plumose setae extending apically, blunt naked tooth like robust setae terminally; outer plate large with apical plumose setae continuous with paired rows of curved facial setae extending medially and submarginally from the base; anteromedial margin carved into sinuosities without marginal robust setae; palp articles 2 and 3 with few lateral setae, moderately setose medially; article 3 without setae or comb rows at base of the dactyl, distolaterally and facially pubescent; apex not produced, dactyl unguiform, multispinous, facially pubescent with short nail and terminal accessory spinule. Coxae 1–7 short, broader than long; coxae 1–4 lacking posterior robust setae; coxa 1 not expanded below; coxa 4 not excavate posteriorly; coxa 5 as long as four. Gnathopods: diverse, dactyls lacking inner tooth like robust seta, lacking nail. First gnathopod: small, feeble, carpus equal to propodus, not lobate, merus lacking hyaline lobe, without rastellate seta, palm transverse, robust setae not symmetrically bifid, rather with small subapical trigger like extensions; armaments at corner of palm few lateral and medial robust setae, setae along palm sparse and simple. Second gnathopod: enlarged, 3.3× gnathopod 1; carpus short and lobate, hand enlarged and ovate, palm strongly oblique, spinose and irregularly setose, defining corner with strong lateral and medial robust setae. Peraeopods: three and four of proportions similar to peraeopods 5–7; posterior robust seta sets on article 6 of peraeopods 3 and 4 unevenly spaced; peraeopods 5–7 moderately long, peraeopods 6 and 7 subequal, longer than five, article 2 moderately expanded, ovatorectangular, posteroventrally extended, slightly lobate on peraeopod 6, lobate on peraeopod 7; dactyls of peraeopods lacking accessory spinules. Coxae 2–6 each with a single flask-shaped gill, that of coxa 6 not reduced. No sternal gills. Oostegites: present on coxae 2–5; thin, strap like, poorly setose. Epimera: posteroventral tooth of epimera 1 to three absent; posterior margins smooth to sinuous with few setae; epimera 2 and 3 with facial robust setae near the ventral margin. Pleopods: peduncles with few setae, rami extending equally, basomedial setae of inner rami not bifid; retinaculae two per pleopod, no accessory robust setae. Uropods: apicolateral corner of peduncles of uropods 1 and 2 with one or two robust setae; mediodorsal margin of peduncle of first uropod spinose, of second naked, mediodistal margin of first uropod with two robust setae; first uropod with basofacial robust seta; lateral rami of uropods 1 and 2 shorter than medial, rami of both uropods mostly with two robust seta rows; third uropod: strongly extended, peduncle short, outer ramus large, inner ramus short, scale like, medial setae of outer ramus sparse, peduncular robust setae few, medial and distal. Urosome: ventrodistal robust seta on urosomite 1 at base of uropod 1 absent. Telson: longer than broad, cleft 90%, laterally convex, bearing, short, marginally subapical setae with one or two long lateral penicillate setae and small, paired lateral penicillate setules.

Relationship. It is difficult to determine the relationship of *Norcapensis* to other melitids, and as an ongoing taxonomic review of the Melitidae is underway (Lowry, pers. com.) it would be premature to speculate on this. However, attention should be drawn to the presence of eriopisid characters, including: absence of eyes; medial setosity of the maxillae; symmetricity of the first maxilla palps; dissimilarity of the gnathopods; non-lobate fourth coxa; peduncular basofacial spine present on the first uropod; elongate third uropod; and deeply cleft, apically notched tapering telson bearing few setae. Among the three eriopisid genera, *Norcapensis* has several characters in common with *Victoriopisa* Karaman & Barnard, including: fusion of the basal articles of the flagellum of the second antenna; seven denticulate apical spines present on the outer plate of the first maxilla; elongate carpus and transverse, convex palm on the first gnathopod; broad, ovate coxal gills. The genus differs, however, from *Victoriopisa* in that: C setae are present and A setae absent from the mandibular palp; inner plate of the first maxilliped is ovate rather than ovatotriangular; fourth article of the seventh peraeopod is not dilated; outer ramus of uropods 1 and 2 are shorter than inner.

This genus appears related to *Nedsia* Barnard & Williams, a marine invader or "crawlout" from the lowland coastal plains of North West Cape and Barrow Island (Barnard & Williams, 1995; Bradbury & Williams, 1996a). *Norcapensis*, nevertheless, differs from *Nedsia* in several minor ways: relatively short first and third articles of the peduncle and the longer flagellum of the first antenna; the upper lip is not excavate below; there are three rather than two articles of the mandibular palp; a greater number of setae on the inner plate of the first maxilla; setae of the outer plate of the maxilliped are not blunt and are more numerous and the distal plumose setae are not accompanied by a bent naked medial robust seta, the apex of the maxillipedal palp is not produced even weakly and the dactyl bears additional accessory setules. The carpus of the first gnathopod is equal in length to the propodus rather than longer, with reduction in the length of the lateral setae at the palmar corner and greater numbers of setae and robust setae along the palm; the second gnathopod is enlarged with a strongly oblique and more setose palm, the palmar corner marked by two or three stout lateral and medial robust setae rather than a single robust seta; the sixth periopod is subequal to the seventh, article 2 of peraeopods 6 and 7 is progressively lobate rather than without lobes as found in *N. douglasi* Barnard & Williams. There are additional setae on the peduncle of the pleopods and

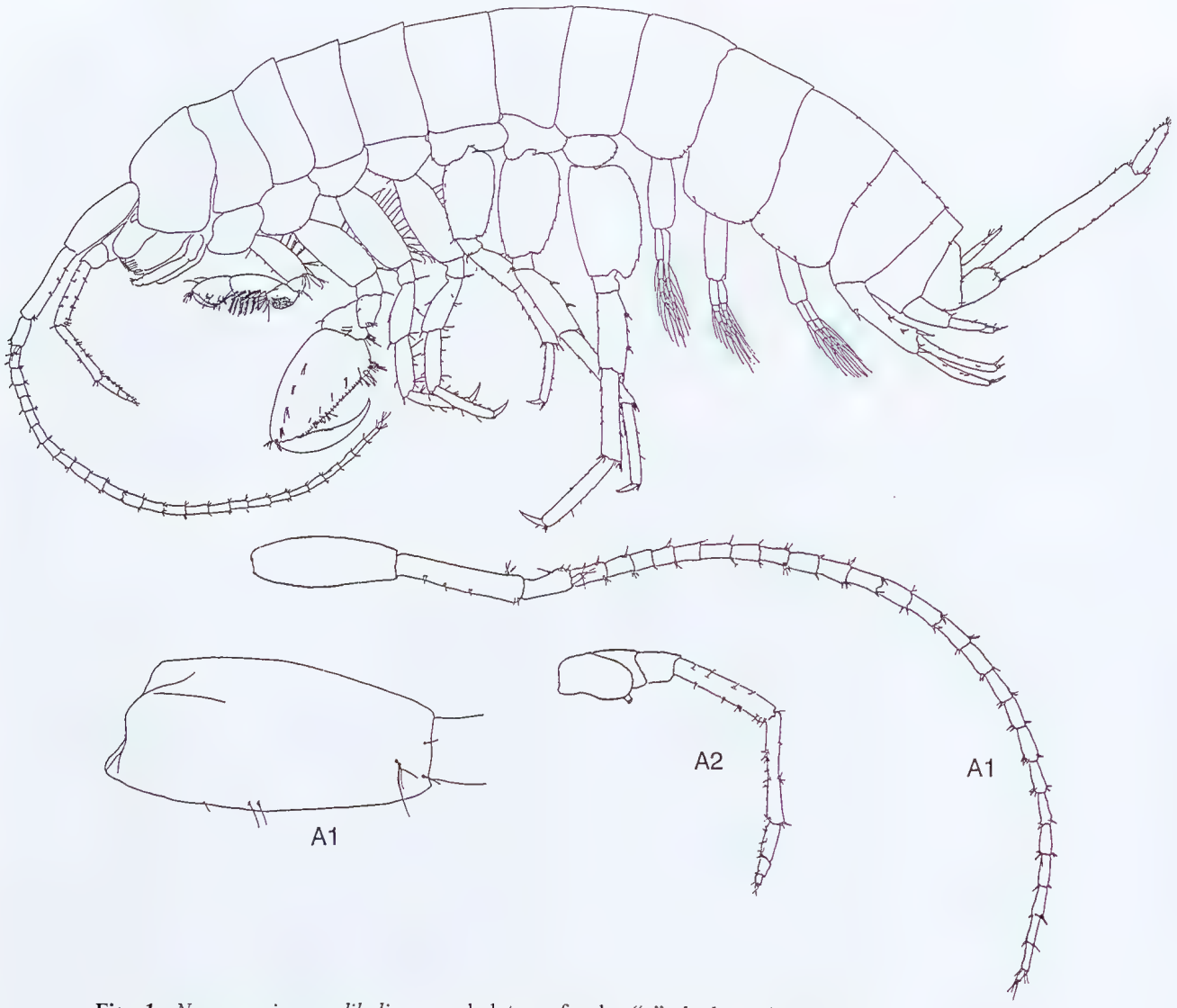

Fig. 1. *Norcapensis mandibulis* n.sp. holotype female "p"; body and antennae.

the rami are equal with no accessory robust setae to the retinacula; the medial margin of the peduncle of the second uropod is without robust setae and the medial ramus bears a single, rather than two robust seta rows; the inner ramus of the third uropod is reduced and the outer ramus long and slender rather than phyllode-like. The telson of *Norcapensis* is cleft 90% rather than 100%, as in *Nedsia*.

The relationship of *Norcapensis* with the other hadzioid genus (*Brachina* Barnard & Williams, 1995) from Australian fresh waters is less close. The genus differs from *Brachina* in: mandibular palp is well developed; lower lip bears inner lobes; inner plate of first maxilliped is ovate, medially setose and pubescent; palp of maxilliped distofacially pubescent and inner plate basofacially pubescent; coxae reduced, all of about the same length; gnathopods and peraeopods 1 and 2 bearing long posterior setae on the second article, dactyls of peraeopods without nail; second article of third uropod elongate; telson slender, with few apical robust setae or setae, cleft 90% rather than 100%.

Norcapensis mandibulis n.sp.

Figs 1–4

Etymology. Named for the presence of well-developed mandibular palps.

Type locality. Underground water, Cape Range, North West Cape, Western Australia.

Material examined. Cape Range, Western Australia. HOLOTYPE (WAM 511-97) female "p" 10 mm, in type series; ALLOTYPE (WAM 512-97) male "t" 12 mm, 7 other female PARATYPES (WAM 513-97), Western Australia Museum: collection CR1989 3236, in gravel in freshwater pool in deep limestone cave, 22°07'S 113°59'E, collected by hand net, R.D. Brooks, 23 June, 1989. Other material: female "q" 10 mm (WAM 514-97), and 4 other females (WAM515-97); station CR1989 3241, in freshwater canal outflow of limestone cave, 22°09'S 114°00'E, collected by hand net, R.D. Brooks, 29 June, 1989; female "r" 9 mm (WAM 516-97) and 2 other females (WAM 517-97), station CR1989 3212, freshwater pool in deep limestone cave, 22°05'S 113°59'E, collected by hand

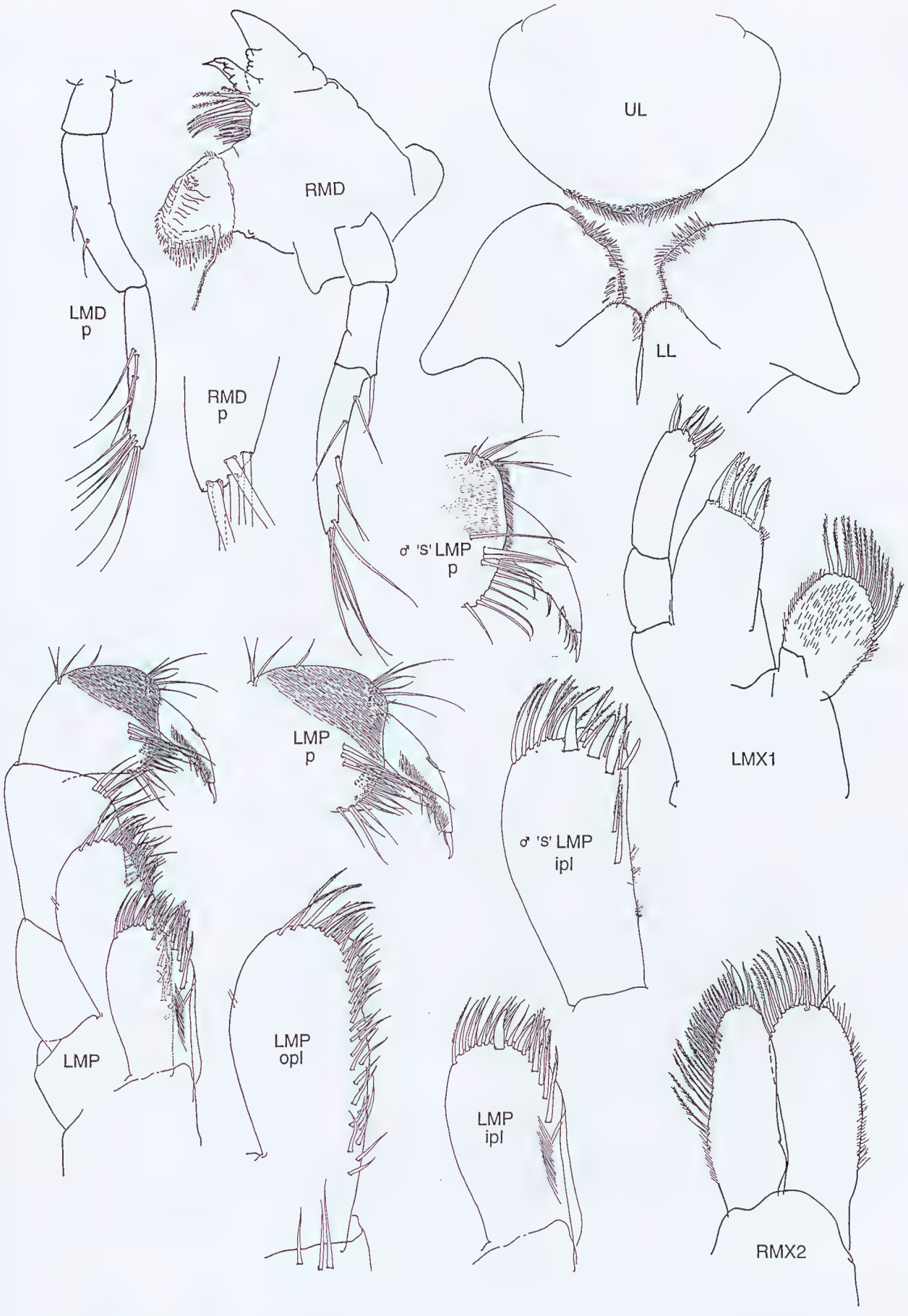

Fig. 2. *Norcapensis mandibulis* n.sp. holotype female "p"; mouthparts (all drawings except those indicated). Male "s" maxilliped inner plate and palp.

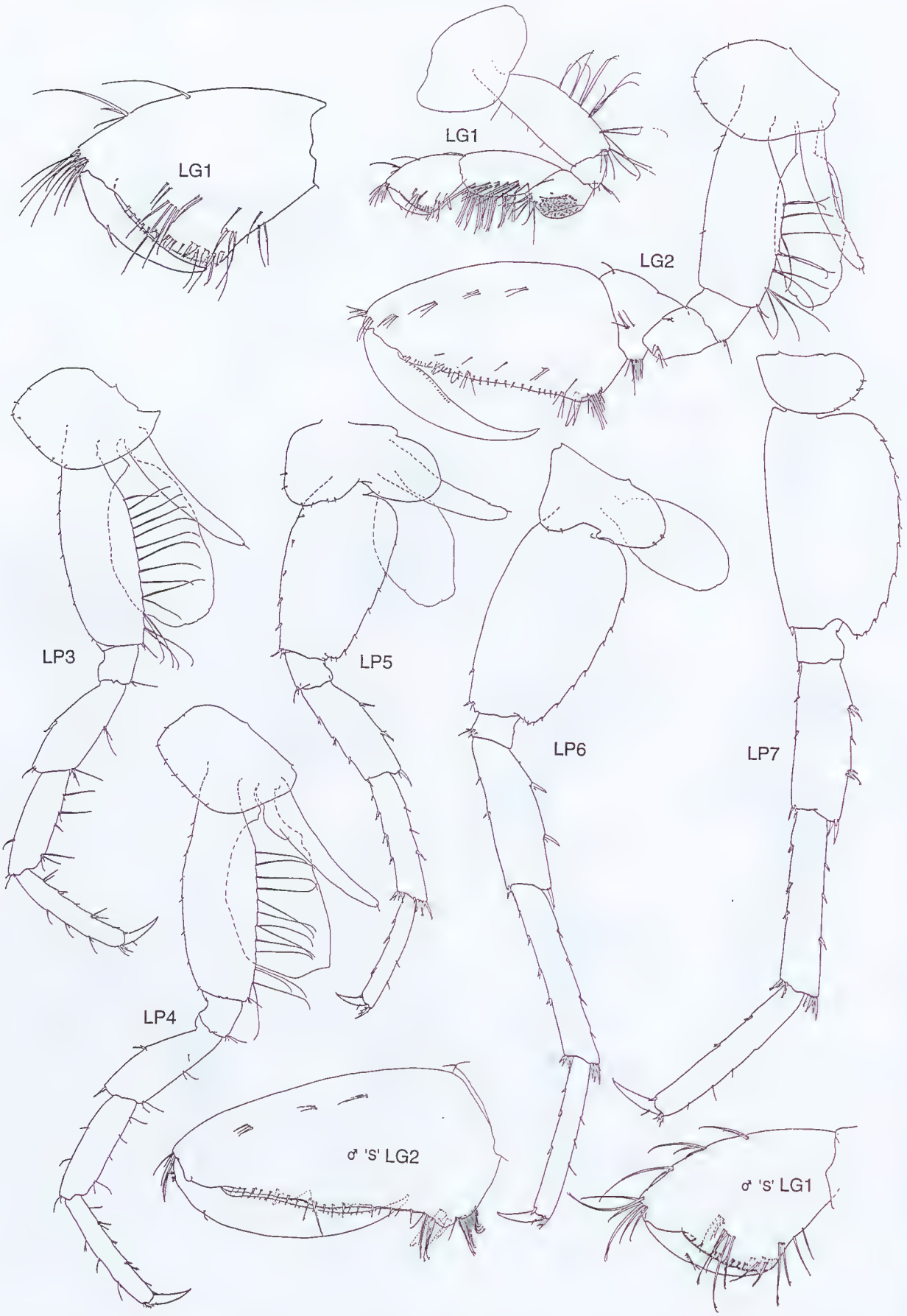

Fig. 3. *Norcapensis mandibulis* n.sp. holotype female "p"; legs (all drawings except those indicated). Male "s" propodus gnathopods 1 and 2.

net, B. Vine, 26 June, 1989; male "s" (WAM 518-97) and 8 females (WAM 519-97), station CR1989 3225, freshwater pool in deep limestone cave, 22°03'S 114°01'E, collected by hand net, B. Vine, 27 June, 1989.

Diagnosis. As in the genus.

Description of holotype (female "p"). *Body* (Fig. 1): urosome poorly armed dorsally, length 10 mm. *Head*: rostrum obsolescent, eyes absent. *First antenna* (Fig. 1): length about 0.7× body, 2.7× second antenna; flagellum longer than peduncle, of 26 articles; peduncle articles 1 and 2 approximately equal, 1 longest, 3 shortest, article 1 with few robust setae or setae, bearing a mediodistal group of three setae but no robust seta, setae sparse on articles 2 and 3; calceoli and aesthetascs absent; accessory flagellum two-articulate, small, second article tiny, extending to M0.5 on first article of primary flagellum. Primary flagellum articles uniform, sparsely setulate. *Second antenna* (Fig. 1): length 0.2× body, peduncle much longer than flagellum, articles 4 and 5 equally long, sparsely setulate, other articles with few setae or robust setae; flagellum short, 5-articulate, few setae, lacking calceoli. *Upper lip* (Fig. 2): symmetrical, ovate, apically pilose. *Lower lip* (Fig. 2): bi-lobed, outer lobes with spinous setae and pilia medially, inner lobes distally pilose. *Left mandible* (Fig. 2): palp three-articulate, ratio of articles 5:7:14, article 1 naked, article 2 linear, subequal to article 1 with two medial setae, article 3 sublinear lacking A or B setae, with 3C1D5E setae; incisor five-teeth, lacinia mobilis six teeth, molar with distal plumose seta and peripheral posterior pubescence. *Right mandible* (Fig. 2): similar, palp ratio of articles 5:13:13, article 2 bearing a single distal seta, setae of article 3 3C1D7E. *First maxilla* (Fig. 2): left and right sides asymmetrical; inner plate ovate to round bearing fourteen plumose apical setae, covered in short pubescence; outer plate bearing seven denticulate terminal robust setae on the left side, ten on the right; palp article 2 terminating in ten long robust setae on the left, eight on the right. *Second maxilla* (Fig. 2): lateral edge of outer plate and basomedial margin of inner plate pubescent; outer plate terminating in 13 long plumose setae (the spinules being restricted to the medial face), and one short naked seta; inner plate bearing five long terminal setae, some naked robust setae mediodistal to distal, and many plumose medial setae extending mediodistally on the face. *Maxilliped* (Fig. 2): peduncle bearing three facial robust setae basal to inner plate; inner plate bearing a medial submarginal row of pubescence; palp article 3 with a row of medial robust setae progressing to submarginal/facial distally, a single distomedial robust seta basal to the dactyl, and two rows of subdistal facial robust setae; adjacent the apex a row of seven robust setae marginal to ventrofacial; distal face covered in non-organised fine setae. *First gnathopod* (Fig. 3): coxal plate with two small setae, one anterodorsal and one ventral; article 4 posteriorly bulbous, but not lobate, covered in short pubescence; article 5 subquadrate, not lobate, bearing clusters of slender robust setae; propodus trapezoidal, expanded apically, longer than wide, few posterior robust setae, cluster of eight robust setae terminally at dactyl base; palmar corner defined by four stout medial robust setae (the first three evenly spaced) and two slender lateral robust setae, palms convex, transverse to slightly oblique, setae along palm small, slender, mostly submarginal, row of fine robust setae proximal to corner; dactyls without medial spination, length short of palmar corner. *Second gnathopod* (Fig. 3): coxal plate broadly rounded, few anterior and one ventral setae; article 4 posteriorly expanded; carpus moderately lobate; propodus enlarged, 3× first gnathopod, ovate, longer than wide, with a row of clusters of facial robust setae dorsally and ventrally; palm strongly oblique, palmar corner rounded, marked by a pair of moderately long, stout robust setae, robust setae along palm mostly small, with triggers, and a pair of distal stout, blunt robust setae; dactyl short of palmar corner, with a submarginal row of small trigger robust setae along the proximal edge. *Peraeopods* (Fig. 3): peraeopods 3–5 equal in length, longer than gnathopods; coxa 3 rounded, subquadrate, slightly broader than long, few marginal setae anteriorly and ventrally; coxa 4 similar, slightly broader, not posteriorly excavate; coxae 5–6 bilobed, small, irregular, coxa 5 without posterior setae, coxa 6 with two small posterior setal robust setae; coxa 7 lacking anterior lobe, with four small posterior robust setae. Peraeopods 3 and 4, article 2 with long, straight, distally curved posterior setae, articles 3 and 4 with few to moderate armaments, articles 5 and 6 with mixed robust setae and setae, the posterior robust seta formulae of articles 6 = 2s,sS,S,3s,S,S and s,3s,2s,2S,s,S with only single locking robust setae on each. Peraeopods 5–7, article 6 armaments few, articles 2–5 moderately spinose with strong apical spination on article 5, dactyls without accessory robust setae except for a single outer penicillate setule. *Gills*: those of coxae 2–6 flask-shaped, that of coxa 6 not reduced. *Oostegites*: present on coxae 2–5 and simple, strap like, poorly setose. *Pleopods* (Fig. 4): each bearing two retinacula with no accessory robust seta, rami equal in length; peduncle of second pleopod with three short median, one apicoposterior and one apical seta, basal articles of rami each with one seta; peduncle of pleopod 3 bearing one mid-median, one apicomedial, one apical and one short apicoposterior seta; rami with one to two setae on basal articles. *Epimera* (Fig. 4): 1 and 2, post-ventrally rounded, bearing five and three small robust setae respectively, epimeron 2 with one moderate anteroventral robust seta and one small mid-ventral robust seta; posterior margin of epimeron 1 slightly concave, epimeron three with small rounded extension posteriorly, one small post- ventral robust seta as well as four small to moderate ventromarginal robust setae, one post-dorsal and one posterior dorsolateral small setae. *Pleon*: pleonite 3 bearing single small posterior dorsal and dorsolateral setae; three small dorsal setae on pleonite 4, pleonites 4 and 5 bearing single dorsolateral setae on the posterior margin, pleonite 6 with small posterior robust setae paired dorsolaterally and single robust setae ventrolaterally. *Uropods* (Fig. 4): length of uropods relative to uropod 1—uropod 2 0.5×, uropod 3 1.8×. Uropod 1, peduncle length 1.2× inner ramus, basofacial robust seta present, and a moderate lateral row of 2-1-1-0-1 robust setae the last being subdistal, two small sublateral distal spurs, one large apicolateral robust seta and one large medial sub apical trigger robust seta; rami of subequal length, the inner being the longer, each with lateral and medial rows of two or three robust setae and a cluster of five terminal robust setae. Second uropod smaller than first, peduncle subequal to lateral ramus, bearing two apicolateral and one apicomedial robust setae; outer ramus 0.75× inner with two sparse rows of single marginal robust setae and four apical robust setae; inner ramus lateral robust setae absent, two medial robust setae, terminal cluster of five robust setae. Third uropod, strongly extended, 0.3× body, peduncle short, 0.25× length of article 1 of the outer ramus, bearing a small ventral robust seta at M0.4, a single ventrodistal robust seta, paired mediodistal and laterodistal short robust setae and a pair of short apicodorsal robust setae; inner ramus small, scale-like, 0.5× peduncle, naked except for a single ventrodistal robust seta and a small distal seta; outer ramus elongate, 2-articulate, proximal article linear, sub rectangular, width to length ratio of 0.2, armed with marginal ranks of short robust setae and setae and a

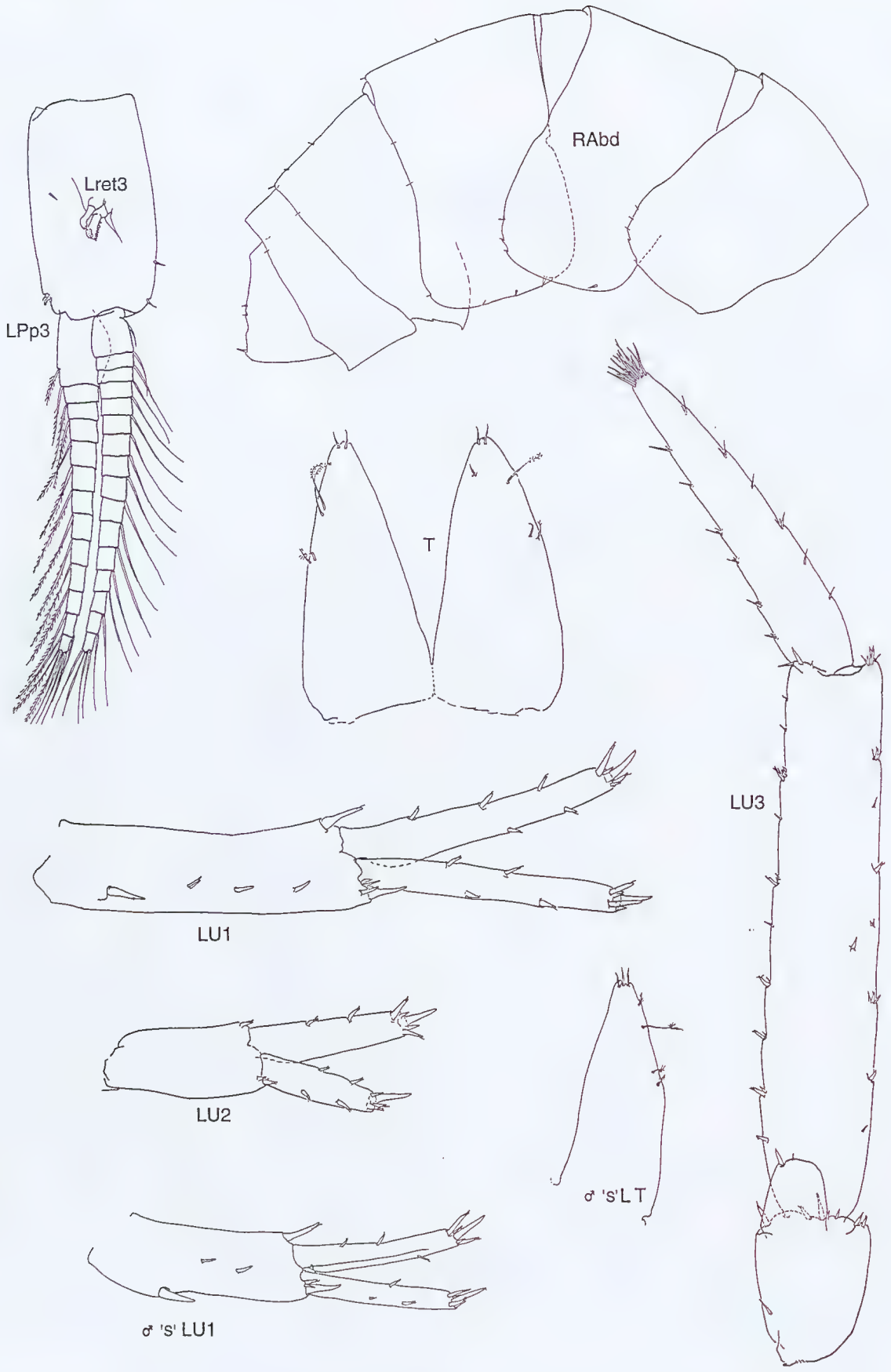

Fig. 4. *Norcapensis mandibulis* n.sp. holotype female "p"; abdomen, pleopod, uropods and telson (all drawings except those indicated). Male "s" left telson.

single facial robust seta at M0.5, a lateral apical cluster of two short robust setae and four setae, the medial apex bearing one robust seta and two setae, distal article 0.6× proximal, slender, similarly armed marginally, tapering from base to apex, terminating in a cluster of 12 slender robust setae. *Telson* (Fig. 4): length twice width, longer than urosomite three (75:60), cleft 90% of length, apices notched, two short marginally sub apical setae on either lobe, with one or two moderately long penicillate dorsal setae at M0.9 and short, paired dorsolateral penicillate setules at M0.7.

Description of allotype (male "t"). *Body*: length 12 mm. *Mandibles*: palps three-articulate, ratio of articles 5:10:12 (cf. 5:7:14 L or 5:13:13 R), setae of article 3 left 4C2D5E, right 1C1D4E. *Maxillae*: inner plate of first maxilla bearing 12 (cf. 14 in the holotype) plumose apical setae; palp article 2 terminating in long robust setae, 8L,7R (cf. 10,8). *Maxilliped*: peduncle bearing two (cf. 3) facial robust setae basal to the inner plate; inner plate with plumose mediodistal seta replaced with medium naked robust seta on L side palp article 3 apex with five rather than seven ventrofacial/marginal robust setae. *First gnathopod*: six anteroapical robust setae of propodus at base of dactyl (cf. 8). *Second gnathopod*: larger than gnathopod 1 3× (cf. 3.3×); defining corner of palm with three strong medial trigger robust setae, and marginally and laterally two long slender trigger robust setae, two similar but distally serrate, and one short slender robust seta distally serrate. *Peraeopods*: article 6 of peraeopods 3 and 4 with posterior robust seta formulae; peraeopod 3: s,2S,s,s2S,s,S and peraeopod 4: 2sS,2s,S,s,s. *Pleopods*: peduncles without setae except a single apicolateral seta on pleopod 2. *First uropod*: peduncle with lateral row of 1-1-0-1 robust setae (cf. 2-1-1-0-1), without small sublateral distal spurs; trigger present on the single apicolateral robust seta, but absent from the medial sub apical robust seta (cf. reverse in the type). *Second uropod*. peduncle bearing a single apicolateral robust seta (cf. 2), outer ramus short 0.7× inner (cf. 0.75). *Third uropod*: peduncle without short apicodorsal robust setae (cf. 2); inner ramus 0.6× peduncle (cf. 0.5) bearing a pair of small distal setae (cf. 1); outer ramus proximal article bearing a lateral apical cluster of three robust setae and three setae (cf. 2&4) the medial apex two robust setae and two setae (cf. 1&2). The distal article terminating in 11 slender robust setae (cf. 12). *Telson*: apices with a single notch, three short, subapical setae on either lobe; plumose dorsal setae at M0.5, 0.6, 0.8; single dorsolateral penicillate setules at M0.7.

Description of other material. Specimen "q", female. *Body*: length 10 mm. *First antenna*: flagellum of 30 articles. *Mandibles*: ratio of lengths of articles of left palp 5:12:11 (cf. 5:7:14), second article not reduced, longer than article 1; setae of article 3 3C2D5E; lacinia mobilis with four teeth, ratio of lengths of articles of right palp 5:10:9.5, setae of article 3 4C1D5E. *Maxillae*: inner plate of first maxilla bearing 13 apical plumose setae, right outer plate bearing 11 denticulate terminal robust setae; outer plate of second maxilla terminating in 12 long plumose setae; inner plate of second maxilla bearing one long terminal seta and many short, curved setae. *Maxilliped*: palp inner plate without facial pubescent row, several distomedial robust setae basal to dactyl and five robust setae adjacent the apex. *First gnathopod*: coxal plate bearing eight small setules; three anterodorsal, one apical, and four ventral. *Second gnathopod*: corner of palm marked by one lateral and two medial robust setae; palmar robust setae include three rather than two stout, blunt distal robust setae. *Peraeopods*: coxa of peraeopod 5 bearing four small submarginal and ventral posterior setae; posterior robust seta formulae of articles 6 of peraeopods 3 and 4 2sS,S,s2S,s,S and s2S,S,s2S,s,S respectively. *Uropods*: lengths of uropods relative to uropod 1; uropod 2 0.6×, uropod 3 2.1×; length of peduncle of uropod 1 1.1× inner ramus; with lateral row of 1-1-1-1 robust setae; outer ramus of second uropod bearing five apical robust setae; lateral robust setae present on inner ramus, and one medial robust seta. Peduncle of uropod 3 with two small ventral robust setae at M0.4, three mediodistal and laterodistal short robust setae, and three apicodorsal robust setae; medial apex of outer ramus bearing two robust setae and three setae. *Telson*: apices bearing a single notch, a single terminal robust seta within the notch, displaced laterally, submarginal robust setae at M0.5 and M0.7, long penicillate setules at M0.9 and short single penicillate setule at M0.7.

Specimen "r", female. *Body*: length 9 mm. *Mandibles*: ratio of articles of palp; 5:12:12, setae of article 3 of left palp 2C3D5E of right palp 3C1D6E; left lacinia mobilis with four teeth (cf. 6). *Maxillae*: inner plate of first maxilla bearing 12 plumose setae, palp article 2 terminating in eight robust setae (cf. 10). *Maxilliped*: peduncle bearing two facial robust setae basal to inner plate; palp with row of five robust setae adjacent the apex. *First gnathopod*: coxa bearing a distal marginal row of six setae, two ventral to the apex, four dorsal; corner of palm defined by two stout medial bifid robust setae (cf. 4) and two slender lateral robust setae. *Second gnathopod*: palm with a single stout, blunt distal robust seta (cf. 2). *Uropods*: uropod 1 peduncle with 0-0-1-1-2 robust setae in lateral row, rami with lateral and medial rows of 1–2 robust seta (cf. 2–3). second uropod; two apicolateral robust setae of peduncle displaced medially, outer ramus with a sparse row of marginal robust setae, inner ramus with one medial robust seta; uropod 3 peduncle without small ventral robust seta at M0.4; inner ramus small, 0.65× length of peduncle, bearing two rather than a single distal seta; proximal article without facial robust seta at M0.5; lateral apical group of two robust setae and three setae; distal article 0.5× proximal (cf. 0.6). *Telson*: apices notched unevenly, one notch displaced laterally, retaining two short marginally sub apical setae on both sides, but with single short penicillates at M0.9

Specimen "s", male. *Body*: length 10 mm. *First antenna*: flagellum of 28 articles (cf. 26). *Mandibles*: palp ratio of articles 5:10:12 (cf. 5:7:14), article 2 naked, incisor of left mandible with six teeth (cf. five), setae of right palp; 2C2D4E. *First maxilla*: inner plate bearing 11 plumose apical setae (cf. 14); left outer plate bearing five terminal robust setae (cf. 7). *Maxilliped* (Fig. 2): peduncle bearing two (cf. 3) facial robust setae basal to the inner plate; inner plate plumose mediodistal seta replaced with medium naked robust seta on left side; palp article 3 apex with five rather than seven ventrofacial/marginal robust setae. *First gnathopod* (Fig. 2): coxal plate with several small submarginal anterior setae rather than one anterodorsal and one ventral seta; propodus with nine rather than eight robust setae in a terminal cluster at the base of the dactyl. *Peraeopods*: coxal plate five bearing a single small posterior seta; coxa 7 with three small posterior robust setae (cf. 4); peraeopods 3 and 4, articles 5 and 6 with posterior robust seta formulae 2sS,S,s2S,s,S and S,sS,s2S,s,S. *Epimera*: posterior margin of epimera 1 bearing three mid-lateral to dorsal small setae; epimeron three with small post-ventral notch, three rather than four ventral marginal robust setae. *First uropod*: peduncle with 1-1-1-0-1 lateral row of robust setae, no sub marginal lateral distal spurs *Second uropod*: peduncle bearing one apicolateral robust seta and a single medial robust seta on the inner ramus. *Third uropod*: peduncle with single (cf. paired) mediodistal

and laterodistal short robust setae and a single short apicodorsal robust seta (cf. 2); outer ramus without facial robust seta at M0.5, but with five rather than three robust setae at the medial apex: distal article short (perhaps regenerate) 0.28× proximal, with few marginal armaments, terminating in a cluster of eight (cf. 12) slender robust setae. *Telson* (Fig. 4): apices with single rather than paired notches bearing single setae; single dorsolateral setae at M0.6, M0.7 and M0.9. *Penis*: paired penial processes laterally on sternum adjacent coxal plates of P7.

Distribution. Cape Range, North West Cape, Western Australia.

Neoniphargidae Bousfield, 1977

The family Neoniphargidae was established by Bousfield (1977). It was subsequently redefined by Bousfield (1982) and by Williams & Barnard (1988) who reduced it to one of entirely Australian content. In their redefinition, Williams & Barnard (1988) eliminated several earlier characters, but introduced two new and significant ones: dendritic sternal gills, and rugosities on gnathopods and maxillipedal palps. Gnathopodal and maxillipedal rugosities were recognised as characters common to all known neoniphargids. Bousfield (1977, 1982) had earlier recognised dendritic gills as a frequent, but not obligatory, character. However, Williams & Barnard (1988) foreshadowed further familial emendment stating (p. 115f) "... we recognise the case for a more formal re diagnosis of the Neoniphargidae—but—given the likelihood of discovery of further neoniphargid species in Australia (and thus familial emendation), we do not consider it appropriate to do this at present."

We describe herein two new genera (*Neocrypta*, *Wombeyanus*) and seven new species. All of these we consider to be neoniphargids. However, they do not exactly fit the family diagnosis as outlined by Williams & Barnard (1988) in so far as they do not bear dendritic sternal gills. Furthermore, in addition to these new genera and species we possess numbers of both epigean and hypogean species from Tasmania, Victoria, and New South Wales, yet to be described, which also have simple gills but which are otherwise undoubted neoniphargids. In a separate study (Bradbury, *et al.*, in press), we confirm the taxonomic significance of gnathopodal and maxillipedal rugosities as definitive diagnostic markers for the family. These rugosities are found on the new species as well as all known neoniphargids.

We believe that a definitive family diagnosis is not possible at this stage of knowledge of Australian neoniphargids. However, it is clear that for practical purposes some further emendation is appropriate even now. Accordingly, the family Neoniphargidae is redefined, taking into account the earlier works of Bousfield (1977, 1982) and Williams & Barnard (1988), the characters of known species, and those displayed by new genera and species described in this report: antennal sinus of head weak or absent; molar of mandible well developed, triturative; outer plate of maxilla 2 with one kind of seta apicolaterally; outer plate of maxilliped of ordinary size; rugosities present on maxillipedal palp and gnathopods; gnathopods small or of medium size, almost mittenform, first not dominant, carpi short and post-ventrally lobate or bearing keel, propodi attached to carpi normally, robust setae on palms not of bifid crangonyctoid form; posterior lobes of coxae 5–7 dominant; oostegites narrow to broad; sternal gills 2–6 present; urosomites separate; inner ramus of uropod 3 present as well as short article 2 of the outer ramus; telson cleft, with few robust apical setae, lobes truncate, apically notched.

No previously described neoniphargids are confirmed troglobites. Differences observed among the new species we report here, including morphological modifications such as loss of eyes and attenuation of bodies, are characteristic of troglobites (Holsinger, 1994a). Exclusion from the family definition of characters such as body form and possession of eyes (Williams & Barnard, 1988), previously included by Bousfield (1977, 1982), is therefore supported. Bousfield (1982) defined the third uropod as short; we find the third uropod long in several species, considering it an adaptation to troglobitic habit (Holsinger, 1994a). However, it is noted an inner ramus is always present, and that the outer ramus always bears a second, albeit small, article. These conditions of the character are noted. Simplification of sternal gills has not been attributed to troglobitic adaptation, yet reduction of dendritic to "incipiently dendritic" gills has been observed in the troglophilic *Wesniphargus nichollsi* (Straškraba); the troglobitic *W. yanchepi* n.sp. and *Jasptorus solepti* n.sp., both bearing lumpy or "incipiently dendritic" sternal gills, are reported here. Furthermore, the sternal gills of even *Neoniphargus* are not wholly dendritic; anterior gills are simple, and fully dendritic sternal gills occur only on the more posterior sternites. Bousfield (1982) considered dendritic gills frequent rather than obligatory among neoniphargids, thus we remove the dendritic condition as an essential familiar character. The telson of some new species described here is cleft less (14–20%) than among previously known neoniphargids (50–75%), which Bousfield (1982) considered significant. However, the telson of these new species is otherwise similar, with truncate, notched lobes, few apical robust setae, and a pair of dorsal setae in most cases; certain characters of the telson are taken into account.

Neocrypta n.gen.

Etymology. Named for the family, and for the cryptic habit of the genus.

Type species. *Neocrypta primaris* n.sp.

Diagnosis. Pleonites with weak dorsal arms; rostrum small; lateral cephalic lobes weakly to moderately projecting; antennal sinus weak to moderate; eyes absent. First antenna: elongate, longer than second antenna, ratio of lengths of peduncular articles 10:9:5 to 10:13:8, accessory flagellum two-articulate, calceoli absent. Second antenna: peduncle and flagellum without calceoli. Mandibular palp; ratio of articles 8:11:12 to 8:18:17, article 2 naked, article 3 weakly falcate to linear, setae DE, rarely CDE. Labium without inner lobes. Maxillae inner plates not setose medially; first maxilla inner plate

ovatotriangular with two, rarely three apical plumose setae, the outer plate with seven robust setae, the palps asymmetric—left side with thin apical robust setae, the right side broad, with thick apical robust setae, not fused to the article; second maxilla inner plate with no oblique row of facial setae, but upper member of 1–2 main medial setae slightly submarginal, or not. Maxillipedal palp article 3 with a rugose apical lobe. Coxae 1–4 elongate, sparsely to moderately setose ventrally; coxae 1–3 lacking a posterior row of robust setae; coxa 1 weakly tapering below or not; coxa 4 with shallow emargination; coxa 5 much shorter than coxa 4. Gnathopods small, sexual dimorphism minor, carpi short and lobate, articles 2–4 both with or without a posterior rugose lobe, palms slightly oblique and convex, bearing rugosities, three robust setae at the palmar corner, occasionally four, robust setae along palm sparse to moderate, without triggers, dactyls with stiff spinules at inner nail articulation, with additional spinules along inner dactyl margin. Peraeopods 5–7 moderately elongate, subequal, article 2 broadly expanded, ovate, and weakly to moderately post-ventrally lobate. Peraeopods 3–7 with one marginal and one facial dactylar setules. Coxae 2–6 with sac like gills; sternites 2–6 bearing simple gills without dendricities or lumps. Pleopods reduced; rarely the outer ramus of moderate length and article number, most with one, rarely two articles on the inner ramus, with no or one marginal setae, and two terminal setae, and reduced numbers of articles on the outer ramus; peduncles each with two retinaculae, no accessory retinaculae. Epimera postventral tooth short or absent, some with facial robust setae near the vent margin, posterior margins weakly setulate. Peduncles of uropods 1 and 2 with one subapical robust seta on the apicomedial corner, of moderate length, not long with a complex tip. Basofacial arms absent from the first uropod, rami of both uropods extending unequally, their margins variably spinose, the inner rami usually with one robust seta row, the outer rami one or two rows, never with dense spination. Third uropod strongly extended, parviramous, the peduncle short, outer ramus 2-articulate, the second article very short, the first article without setae, the inner ramus reaching to M0.13 or less of article 1 of the outer ramus. Telson moderately long, cleft 11–20%, the lobes basolaterally weakly tumid with apical and in some mid lateral spination, no major setation or basofacial armaments, paired lateral penicillate setules at M0.6 on either lobe.

Additional description. Upper lip uniform, rounded but weakly asymmetrical below. Mandibular accessory blades (rakers) usually with interraker plumose setae. Very few additional penicillate setae beyond rakers riding onto the base of the molar, rather two to four basal molarial ragged setae. Lower lip uniform, inner lobes indistinct or absent, second maxilla—both plates with long apical setae. Maxillae inner plates and the lateral margins of the second maxilla moderately pubescent. Maxilliped inner plate with few distal plumose setae, two or three blunt naked robust setae, few or no medial plumose setae. The outer plate with a distal row of few plumose setae continuous with a distal row of blunt naked tooth like robust setae. Palp articles 2 and 3 poorly setose laterally, well to moderately setose medially, article 3 with a few non comb robust setae near the base of the dactyl. Dactyls of gnathopods with or without recumbent inner tooth like robust seta with stiff spinules or setules at the inner nail articulation, sometimes with additional spinules along the inner dactylar margin. Pleopods similar, peduncles not strongly setose, rami diverse, inner ramus strongly reduced. Urosomite 1 without an articulated ventrodistal robust seta at the base of the first uropod.

Relationship. The new genus *Neocrypta* is most closely related to *Neoniphargus* (Stebbing), but differs in the following: eyes are absent; the first article of the mandibular palp is relatively long, the second is naked, the third without A or B setae; coxae 1–4 are not as long, and coxa 4 less deeply emarginate; gnathopodal palmar robust setae are simple; thoracic segments 2–6 bear simple rather than dendritic sternal gills; the inner ramus of the pleopods is reduced to one or two articles; the third uropod extends beyond uropods 1 and 2 in the intact specimen and is up to 1.5× the length of the first uropod; the telson is cleft to 20% rather than to 50–75%. As well as in the above characteristics, *Neocrypta* differs from *Wesniphargus* (Williams & Barnard) in that rugosities are borne on propodi of both gnathopods, from *Tasniphargus* Williams & Barnard as antennae bear only short, sparse setae, and the basal articles of the primary flagellum of antenna 1 are short, and from *Yulia* Williams & Barnard in that the pleopod peduncles are not strongly setose, and the outer ramus of male uropod 1 does not bear a long apical spur.

Neocrypta primaris n.sp

Figs 5–9

Etymology. From Latin, *primordius*, the first or most primitive, referring to the type species of the genus and apparently the most plesiomorphic.

Material examined. HOLOTYPE (Australian Museum P51361) female "a" 6.5 mm, ALLOTYPE (Australian Museum P51362) male "c" 6.5 mm. Others in the type series: female "b" 7 mm, and five other specimens. Collected 8 March, 1995 by S. Eberhard from among tree roots in a pool, Limekiln Cave (cave WE14) Wellington, New South Wales, 32°33'S 148°57'E.

Diagnosis. Lateral cephalic lobes moderately projecting, antennal sinus moderate, ratio of lengths of peduncular articles of first antenna 10:12:8; ratio of lengths of mandibular palp articles 8:11:12 to 8:13:14, article 3 linear, setae (C)DE, the inner plate of the first maxilla with two plumose apical setae, inner pate of the second maxilla with two mediodistal submarginal plumose setae. Coxa 1 tapering apically, second article of the first gnathopod and second and third articles of the second gnathopod without posterior rugose hump, robust setae at palmar corner 4-3 respectively, palmar robust setae sparse to moderate, peraeopod 6 longer than seven, articles 2 of legs 5–7 moderately postventrally lobate. outer rami of pleopods moderately long, inner rami strongly reduced, of one article, with few marginal setae. Epimera without postventral teeth, with facial robust setae on the first and second. Uropods 1 and 2 with no more than one robust seta row on rami, inner ramus of third uropod reaching m0.1 of the outer ramus. Telson cleft 16%, with mid lateral spination.

Description of holotype (female "a"). *Body* (Fig. 5): pleon with few dorsal armaments, pleonite 5 with two mid dorsolateral robust setae, six with one posterodorsal robust seta basal to the telson; length 6.5 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 5): length 0.58× body, 2.2× second antenna, peduncle shorter than flagellum, ratio of article lengths 10:12:8, setae sparse, flagellum of 26 articles, aesthetascs present on articles 3–25, flagellar segments uniform,

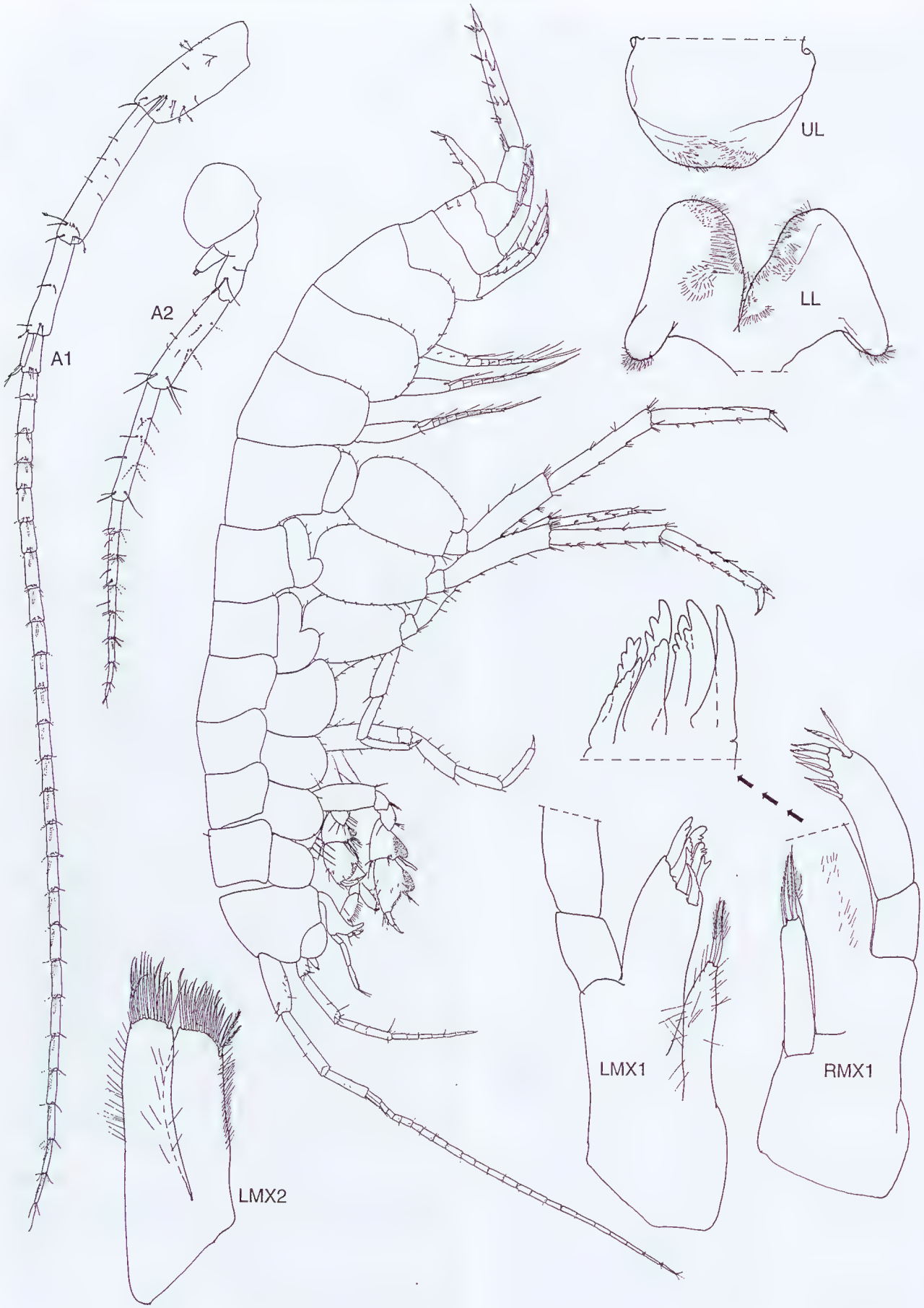

Fig. 5. *Neocrypta primaris* n.sp. holotype female "a"; body, antennae, mouthparts.

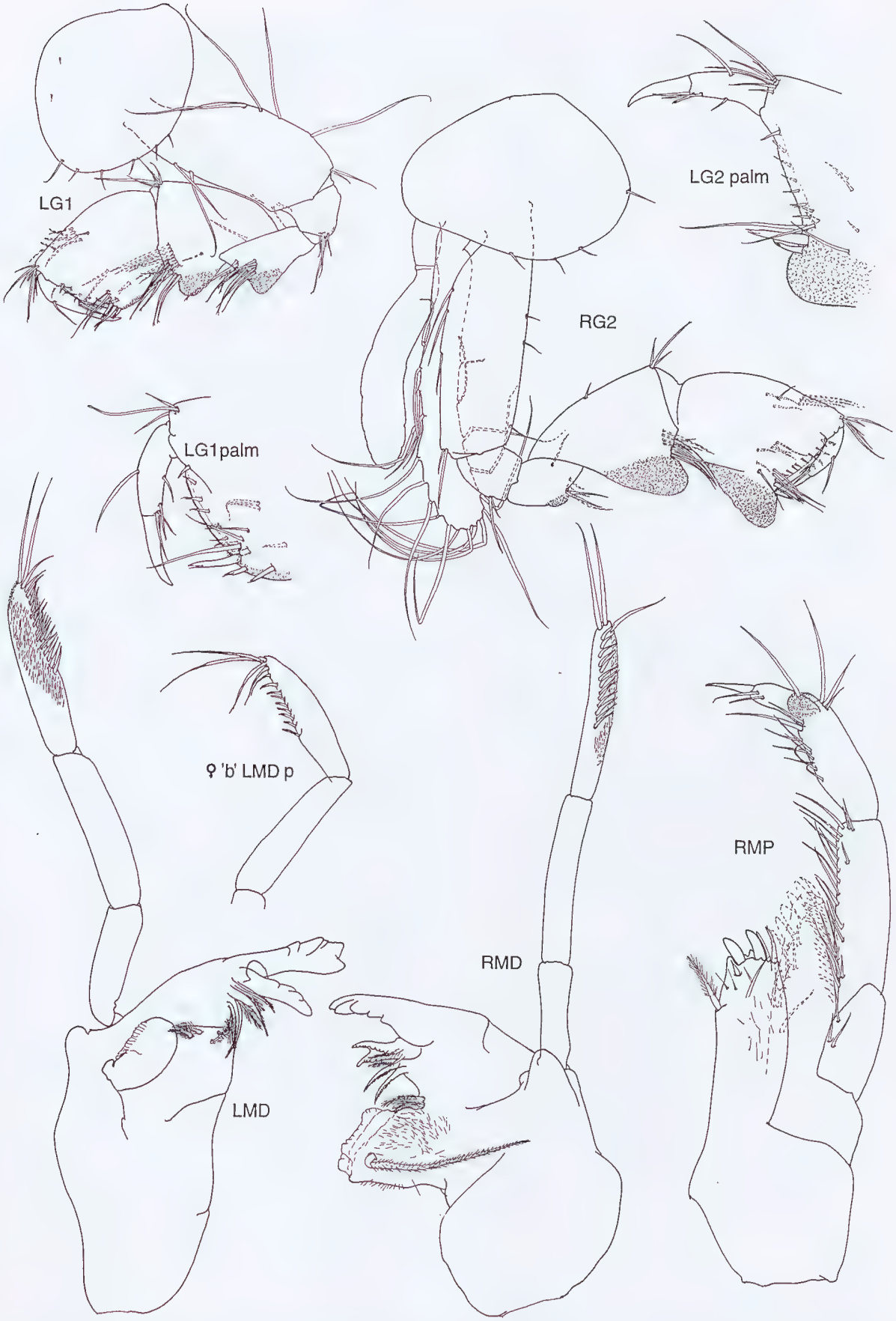

Fig. 6. *Neocrypta primaris* n.sp. holotype female "a"; mandibles, maxilliped, gnathopods (all drawings except those indicated). Female "b" left mandibular palp.

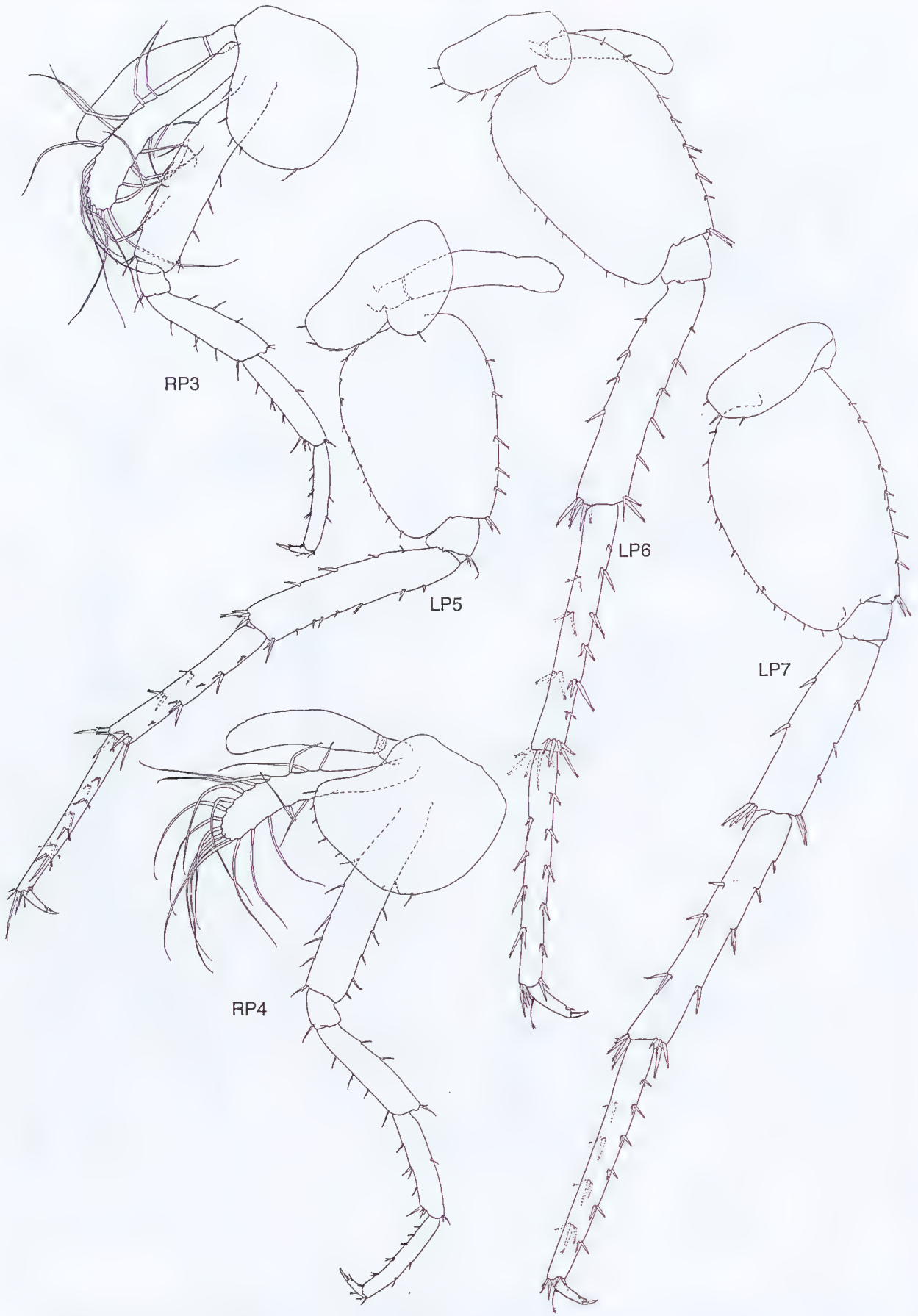

Fig. 7. *Neocrypta primaris* n.sp. holotype female "a"; peraeopods.

sparsely setulate; accessory flagellum 2-articulate, reaching to M0.5 of the second primary flagellum article. *Second antenna* (Fig. 5): length 0.3× body; peduncle 1.9× flagellum, articles 4 and 5 subequal (20:25), articles 3–5 with moderate ventral setation; flagellum of eight articles, weakly setose ventrally, aesthetascs absent. *Left mandible* (Fig. 6): palp article 3 longer than 2, ratio of lengths of articles 8:11:12, article 3 linear, facially and apically rugose, setae 5C14D3E, articles 1 and 2 naked; incisor with six teeth; lacinia mobilis four teeth; accessory blades of three chisel robust setae and three plumose robust setae, four brushy setae onto the base of the molar; molar triturative without a posterior seta. *Right mandible* (Fig. 6): palp article 3 with setae 13D3E, laterofacially rugose; incisor with five teeth; lacinia bifid, denticulate; accessory blades of two chisel robust setae and two plumose setae, two plumose robust setae onto the molar base; molar triturative with a long posterior pappose seta. *Maxillae* (Fig. 5). Left first maxilla: palp article 2 with a row of two naked and one armed mediodistal slender robust setae and three armed transverse apical robust setae; outer plate with seven apically denticulate robust setae; inner plate with two apical plumose setae. Right first maxilla: palp article 2 with a mediodistal row of six strong robust setae, naked and armed, and two laterodistal submarginal armed robust setae; the outer plate with seven mostly denticulate robust setae; inner plate with two apical plumose setae and a moderate, simple sub apical seta. Second maxilla: outer plate with one mediodistal naked seta, inner plate apicomedial corner with two weakly submarginal plumose setae. *Maxilliped* (Fig. 6): palp article 3 without inner ventral setae, moderately setate distomedially, three distolateral setae, two setae basofacial to the dactyl and two accessory spinules on the dactyl, apex moderately produced and rugose; inner plate apex with two thick tooth like robust setae, one distolateral armed and one simple seta, a short stout sub marginal, sub distal seta and one medial plumose seta. *Gnathopods* (Fig. 6): coxal plate of first gnathopod broad, apically tapering, with sparse moderate apical setae; article 2 without posterior rugose extension; article 3 with a small posterior rugose hump; articles 4 and 5 with strong posterior rugose lobes; carpus short, lobe rounded, without apical setae; propodus trapezoidal, as wide as long, the posterior angle sub quadrate with a barely expanded posterior rugose area, palmar corner robust setae one medial, three lateral, palmar robust setae moderate, simple; dactyl with accessory spinules on the inner margin, reaching beyond palmar corner robust setae. Second gnathopopod: larger than the first; articles 2 and 3 without posterior rugose enlargement; article 4 with a small rugose lobe; carpus and propodus with strong posterior rugose lobes larger than on gnathopod 1; palmar corner marked by one medial and two lateral robust setae, palmar robust setae moderately crowded, simple; dactyl with inner marginal accessory setules and small facial setules, reaching the palmar corner robust setae; coxa weakly setose apically, bearing a long sac like gill and long slender setose oostegite. *Peraeopods* (Fig. 7): coxa 3 with three small apical, and two moderate posterior setae, bearing a long sac like gill and long narrow setose oostegite; coxa 4 moderately emarginate with few apical setae; peraeopods 3 and 4 subequal in length, longer than the second gnathopod, articles 4 and 5 moderately setose posteriorly, articles 6 with robust seta formulae 1-1-3-2 and 1-1-2-3-2 respectively; peraeopods 5–7 similar, 6 and 7 subequal, longer than five, coxae with 4-3-4 weak robust setae on the ventral margin of the posterior lobe, coxae 5 and 6 with moderate sac like gills, articles 2 expanded posteriorly (5<6<7) and moderately lobate postventrally, with weak posteromarginal setae; propodi posterior margins lacking long setae except for a long basodactylar seta on leg five. *Gills* (Fig. 8): coxae 2–5 bearing sac like gills; sternites 2–6 each with paired simple gills. *Epimera* (Fig. 8): without postventral teeth, posterior margins slightly to moderately convex with weak setation, ventral margins of epimera 2 and four with three and seven facial robust setae respectively. *Pleon* (Fig. 8): pleonites 1–4 with no arms; pleonite 5 with a strong pair of dorsolateral robust setae; pleonite 6 with a single dorsal robust seta basal to the telson. *Pleopods* (Fig. 8): peduncles each with two retinacula; peduncle 1 with a small distal seta basal to the rami; peduncle three with two laterodistal setae; outer rami of pleopods moderately long with 11, 10, 9 articles, inner rami reduced to single articles, only the first ramus with a marginal seta. *Uropods* (Fig. 8): third uropod long, extending well beyond first and second uropods in the intact specimen; uropod lengths relative to uropod 1; uropod 2 0.8–0.9×, uropod 3 1.9×. First uropod peduncle length 1.3× inner ramus, 2.3× outer ramus; the outer margin with one slightly subapical distal robust seta and a dorsal row of five robust setae, the inner margin with three short dorsal robust setae and one sub apical robust seta; inner ramus length 1.9× outer ramus, with two medial and four apical robust setae, outer ramus with four apical robust setae only. Second uropod: left peduncle with a row of two short dorsolateral robust setae and one sub apical robust seta, the inner margin with one sub apical robust seta; right peduncle with an outer marginal row of four short robust setae and one sub apical distal robust seta, the inner margin with only a sub apical distal robust seta; inner ramus length 1.2× outer, with two medial and four apical robust setae; outer ramus with one lateral robust seta and four apical robust setae. Third uropod: peduncle length 0.3× outer ramus, greater than the length of urosomite three, without facial robust setae, with one distolateral robust seta and one distomedial robust seta basal to the inner ramus; proximal article of outer ramus with five lateral transverse rows of 1-2-2-2-2 robust setae and six medial transverse rows of 1-1-2-2-1-2 robust setae and three medial and three lateral distal robust setae; distal article with two small apical setules only; inner ramus with a single apical robust seta, length 0.09× outer ramus. *Telson* (Fig. 8): moderately long, 1.7× urosomite three, cleft 16%, apices of lobes bearing three right and four left setae, two robust setae laterodorsally at M0.4, paired lateral penicillate setules at M0.6, and small setules on the dorsal face.

Description of allotype (male "c"). *Body*: length 6.5 mm. *First antenna* (Fig. 9): peduncle article 2 longest, ratio of lengths of articles 10:12:8; primary flagellum of 25 articles, all bearing aesthetascs, articles 2, 5, 7, 9, 11 each with two distal aesthetascs, article 4 with three. *Second antenna*: flagellum of seven articles, without aesthetascs. *Mandibles* (Fig. 9): left and right palps similar; naked except for apical setae and rugosities, ratio of lengths of articles 8:14:13, setae of third article 8D4E. Left incisor, lacinia mobilis, accessory blades similar to holotype, molar with one anterior plumose seta, two brushy setae leading to the molar and a moderate posterior pappose seta. Right mandible incisor with five teeth, accessory blades of three chisel robust setae and two plumose setae, with three plumose setae leading to the base of the molar. *First maxilla* (Fig. 9): left palp with four slender armed transverse apical robust setae and two distomedial simple slender robust setae; right palp with four slender distomedial robust setae, and apical slightly stouter distally armed robust seta, and two slender laterodistal armed robust setae; inner plate of both first maxillae with two apical plumose setae. *Second maxilla* (Fig. 9): outer plate with two subdistal lateral

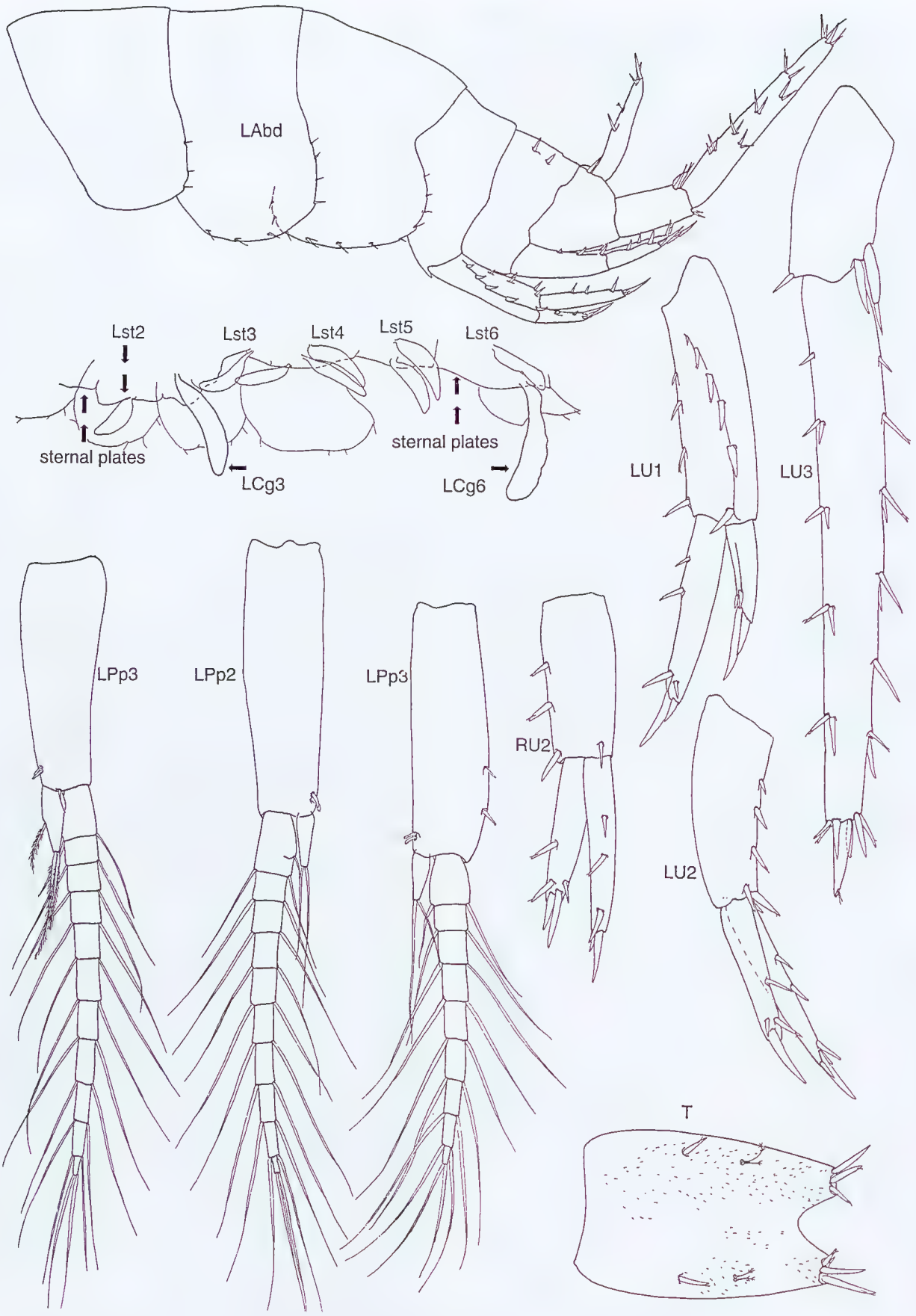

Fig. 8. *Neocrypta primaris* n.sp. holotype female "a"; abdomen, gills, pleopods, uropods, telson.

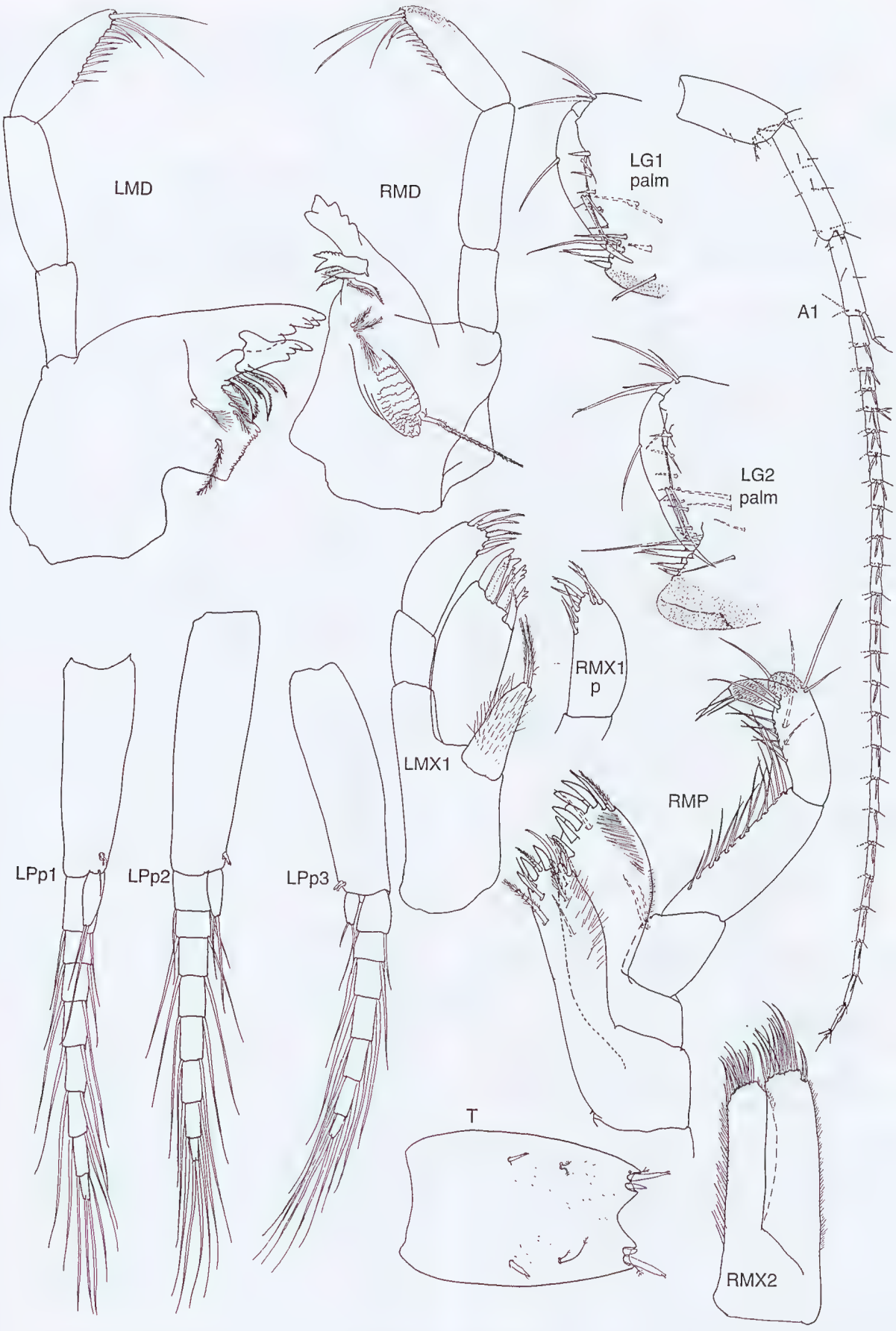

Fig. 9. *Neocrypta primaris* n.sp. allotype male "c"; first antenna, mouthparts, pleopods, telson.

short robust setae, inner plate without two weak submarginal apicomedial plumose setae. *Maxilliped* (Fig. 9): outer plate medial submargin with a row of simple and plumose setae; mid medial to apical face a row of five long naked tooth like robust setae; distolateral margin with slender robust seta and plumose seta. *Pleopods* (Fig. 9): peduncles without arms except a small simple seta basal to the inner ramus on the first pleopod; inner rami each of one article; outer rami of 8, 8, 7 articles. *Telson* (Fig. 9): length 1.5× width; cleft 9%; apices each with one short medial and one longer lateral robust seta and a single lateral penicillate setule; dorsolateral robust setae at M0.4; paired penicillate setules on each side at M0.7; the distodorsal surface with scattered very small setules.

Description of female "b". *Body*: length 7 mm. *First antenna*: with 25 flagellar articles. *Second antenna*: flagellum of seven articles. *Left mandible*: palp third article with small rugosities, setae 9D3E. *Right mandible*: palp article 3 rugose, setae 8D5E. *Pleon*: pleonite 5 with two dorsolateral robust setae, pleonite 6 with one dorsal robust seta basal to telson. *First uropod*: peduncle lateral margin with four dorsal and one apical short robust setae; medial margin with two dorsal and one slightly sub apical robust seta; inner ramus with two medial and four apical robust setae; outer ramus with two lateral, one distomedial and four apical robust setae. *Second uropod*: peduncle lateral margin with two dorsal plus one apical robust seta, medial margin with one small mid dorsal and one apical robust seta; inner ramus with one medial and four apical robust setae, outer ramus with one lateral and four apical robust setae. *Third uropod*: peduncle with only distal robust setae, inner ramus with one apical robust seta, outer ramus proximal article with three lateral ranks of 2-2-2 and three distal robust setae, and four medial ranks of 4-3-3-4 and two distal robust setae; distal article with one small apical spinule. *Telson*: bearing dorsolateral robust setae at M0.5 on either side, paired dorsolateral penicillate setules at M0.7, and with two left and three right apical robust setae.

Distribution. Limekiln Cave, Wellington, New South Wales, 32°33'S 148°57'E.

Neocrypta robinae n.sp.

Figs 10–12

Etymology. Named for the wife of the first author in recognition of her indirect support of amphipod studies.

Type locality. Diprotodon Cave, Cave number CN-10, Canomodine, New South Wales, 33°30'S 148°52'E.

Material examined. HOLOTYPE (Australian Museum P51363) male 6 mm; collected by S. Eberhard; 2 April, 1995.

Diagnosis. Lateral cephalic lobes moderately projecting, antennal sinus moderate, first antenna peduncle ratio of articles 26:24:13, mandibular palp ratio of articles 8:16:16 to 8:18:17, article 3 weakly falcate, setae DE, first maxillae inner plates with two plumose apical setae, inner plate of second maxilla with two distomedial submarginal plumose setae, coxa 1 very weakly tapering apically, gnathopod 1 articles 2 and 3 without posterior rugose hump, gnathopod 2 articles 3 and 4 without rugose hump, palmar corner robust setae 3-3, robust setae along the palm moderately dense, peraeopod 6 longer than seven, articles 2 of legs 5–7 weakly lobate postventrally. Rami of pleopods reduced; inner rami of pleopod 1 with two articles on the right, others with only one article, each with a single marginal seta. Epimera with a small postventral tooth like on the second epimeron only, each with ventrofacial robust setae. Rami of the first and second uropods without dorsal robust setae, the inner ramus of uropod 3 0.1× the length of the outer ramus. Telson cleft 12%, without mid lateral spination.

Description of holotype (male). *Body* (Fig. 10): pleon not armed dorsally except for a single dorsal robust seta adjacent the base of the telson; length 6 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 10): length 0.4× body, 1.2× second antenna, peduncle subequal to the length of the flagellum—63:65—ratio of lengths of the articles 10:9:5, flagellum of 11 articles, uniform and sparsely setulate, articles 1–8 with aesthetascs in pairs, nine to 11 with single aesthetascs, accessory flagellum of two articles, reaching to the end of the first article of the primary flagellum. *Second antenna* (Fig. 10): 0.28× length of body, peduncle much longer than flagellum—79:26—articles 4 and 5 subequal—27:28—articles 3–5 with moderate ventral setation; flagellum of four articles, weakly setose ventrally, without aesthetascs. *Left mandible* (Fig. 10): palp; ratio of lengths of articles 8:16:16, article 3 weakly falcate, setae 17D5E, apex rugose, articles 1 and 2 naked; slender seta at the base of the palp; incisor with five teeth; lacinia mobilis four teeth and fine posterior basal setules; accessory blades of three chisel robust setae and three interraker plumose robust setae, with four brushy setae to the base of the molar; molar triturative, with a short posterior pappose seta. *Right mandible* (Fig. 10): palp article 3 with setae 17D5E, apex rugose; incisor with five teeth; lacinia bifid and denticulate, with an area of setules at the base; accessory blades of two chisel robust setae and one plumose seta, with a short plumose and two brushy setae onto the base of the molar; molar triturative with a long posterior pappose seta. *Maxillae* (Fig. 10). Left first maxilla palp article 2 with one apical and one subapical armed and one naked robust seta, one distolateral plumose seta and two disto medial naked setae; outer plate with seven denticulate robust setae, the inner plate with two apical plumose setae. Right first maxilla palp article 2 with a row of four submarginal mediodistal to apical stout robust setae, the apical two terminally armed, a similar distolateral robust seta and a single distofacial seta; outer plate bearing seven denticulate robust setae; inner plate with two plumose apical setae. Second maxilla: outer plate with a small spinule and moderate seta distolaterally, the inner plate with two submarginal distomedial plumose setae. *Maxilliped* (Fig. 10): Palp article 3 without basomedial and with few distomedial setae, two long setae facio basal to the apex, and a ventral row of three setae basal to the dactyl; apex moderately produced and rugose, dactyl facially pubescent with two accessory spinules basal to the nail; article 2 moderately to well setose medially; apex of inner plate with two thick tooth like robust setae, a stout plumose seta and a naked seta, two ventrofacial setae and one mediofacial seta; outer plate with an apical transverse row of three slender and one stout pappose robust setae, a barely facial medial row of four basally pappose moderate robust setae, a distofacial slender seta and five basomedial setae arranged 1-2-2. *Gnathopods* (Fig. 11): coxal plate of gnathopod 1 with one postventral, one anteroventral and two mid facial setae as well as several small facial setules; articles 2 and 3 without posterior rugose extension, article 4 with a small posterior rugose lobe; carpus short, strongly lobate and rugose posteriorly, the lobe rounded, without apical setae; propodus trapezoidal, longer than wide, the post-lateral edge subquadrate, faintly rugose, with one medial and two lateral

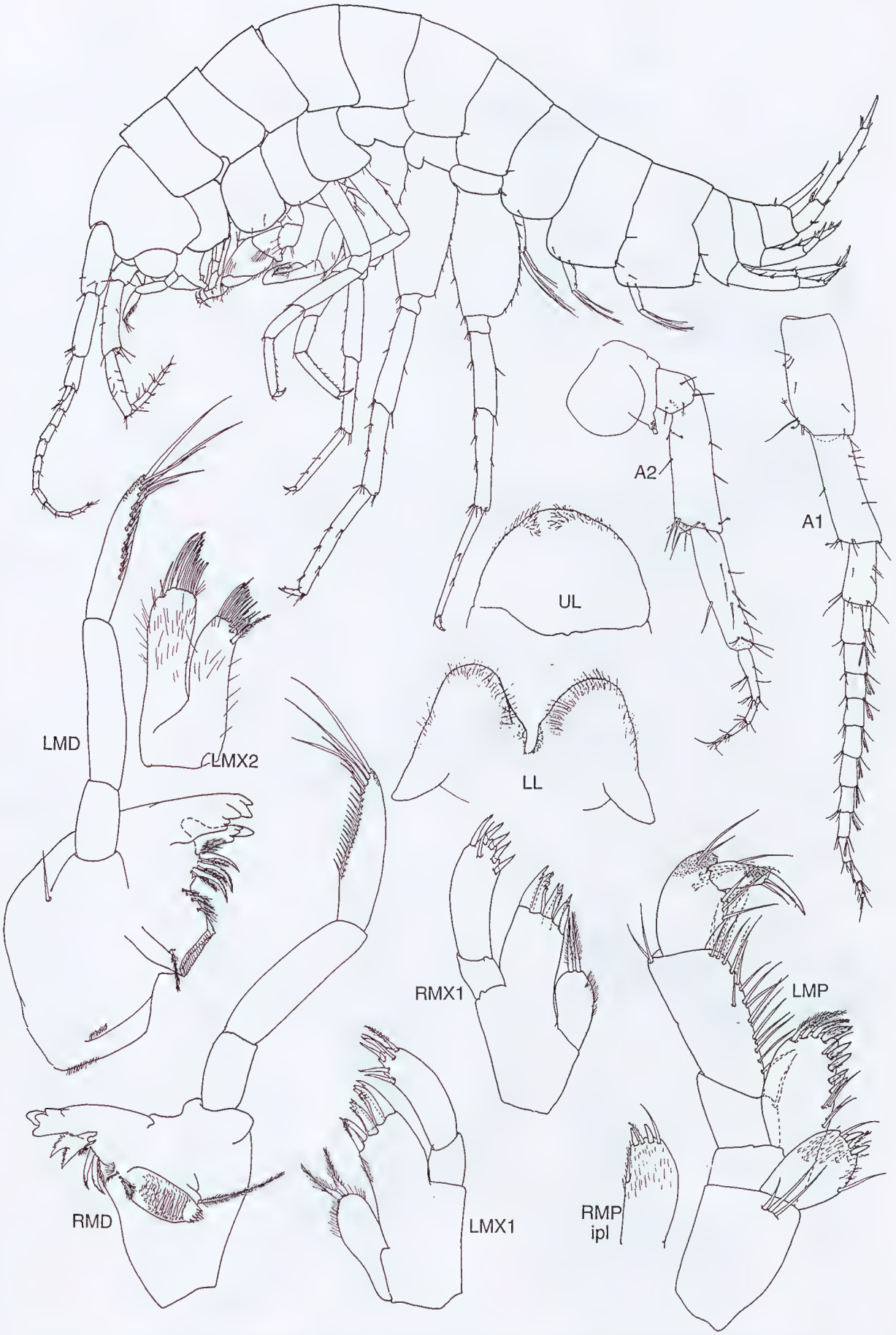

Fig. 10. *Neocrypta robinae* n.sp. holotype male 6 mm; body, antennae, mouthparts.

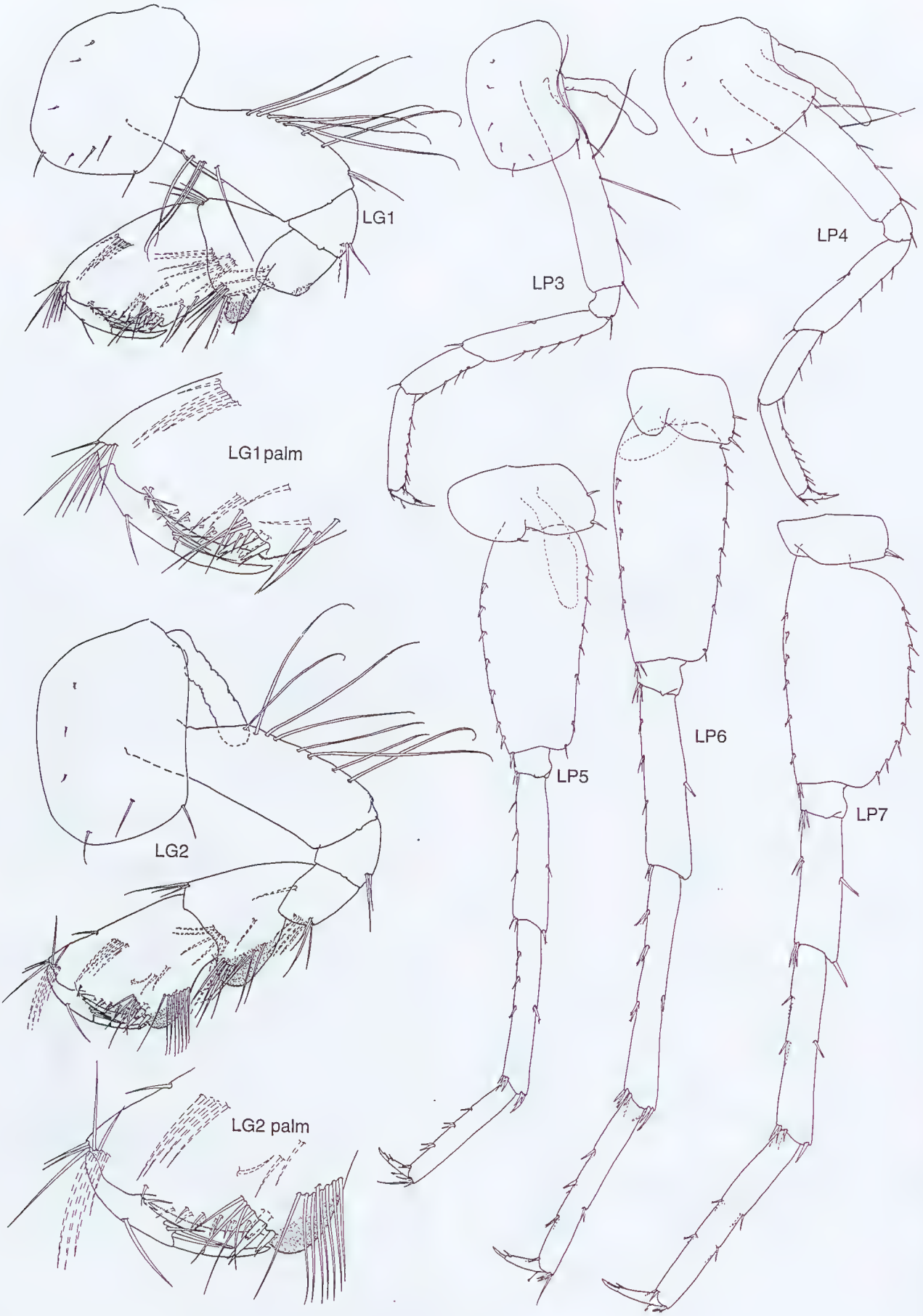

Fig. 11. *Neocrypta robinae* n.sp. holotype male 6 mm; legs.

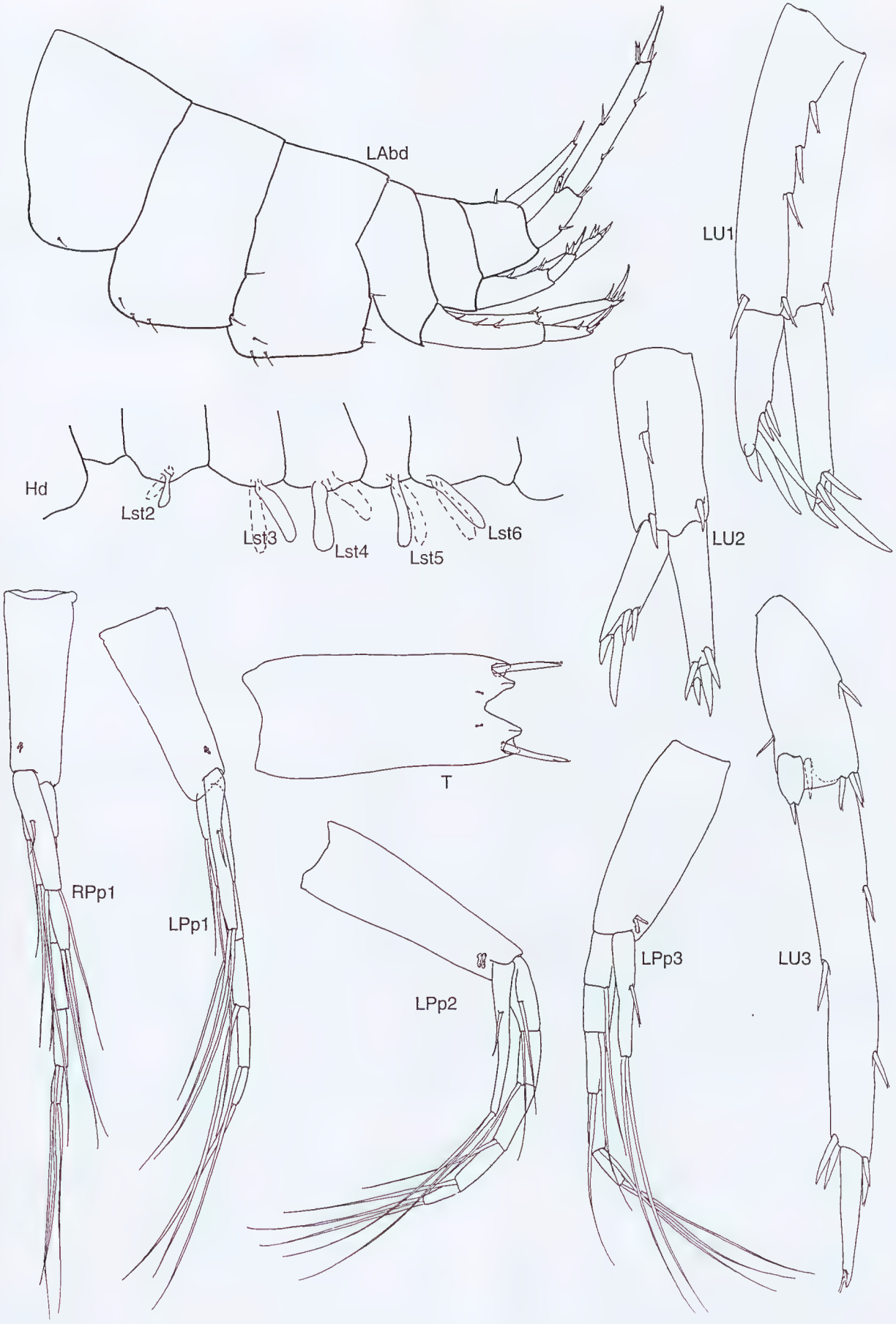

Fig. 12. *Neocrypta robinae* n.sp. holotype male 6 mm; abdomen, gills, pleopods, uropods, telson.

palmar corner robust setae; robust setae along the palm moderately crowded; dactyl with accessory spinules and a small recumbent robust seta on the inner margin, reaching beyond the palmar corner. Second gnathopod: slightly larger than gnathopod 1; article 2 with a small posterior rugose hump, articles 3 and 4 without; carpal lobe broader than gnathopod 1; propodus with distinct posterior rugose lobe, palmar corner with one medial, two lateral robust setae, the palm moderately crowded with robust setae; dactyl with a small proximal recumbent robust seta and accessory setules on the inner margin, reaching to palmar corner robust setae; coxa sparsely setulose apically, bearing a small sac like gill. *Peraeopods* (Fig. 11): coxae 3 and 4 with sparse, weak apical setae; coxa 4 weakly emarginate; peraeopods 3 and 4 subequal, longer than gnathopod 2, articles 3 and 4 weakly spinose posteriorly, propodi with evenly spaced single posterior robust setae; peraeopods 5–7 similar, leg six longest, five and seven subequal, coxae with 2-3-2 robust setae on the posterior margins, second articles expanded moderately, sub quadrate to ovate, weakly postventrally lobate, with weak marginal setation; propodi lacking strong setae on the posterior margins except for long subdactylar setae on legs 5 and 6. *Gills* (Fig. 12): coxae 2–6 with sac like gills; sternites 2–6 with paired simple medial gills. *Epimera* (Fig. 12): second epimeron only with a small postventral tooth; posterior margins of E1–2 almost straight, of E3 convex, the posterior margins weakly setulate; first epimeron with a single mid facial robust seta, the second and third with one anterofacial and two mid ventral robust setae. *Pleon* (Fig. 12): pleonites 1 to six without posteromarginal setae or robust setae, six with a single posterodorsal robust seta adjacent the telson. *Pleopods* (Fig. 12): two retinacula each, peduncles all naked; pleopods reduced, right pleopod 1 with two articles on the inner ramus, all other pleopods with one moderately elongate inner article, each with a single medial marginal seta; outer rami with 6-5-5 articles. *Uropods* (Fig. 12): third uropod extending well beyond uropods 1 and 2 in the intact specimen; uropod lengths relative to uropod 1, uropod 2 0.68×, uropod 3 1.4×; first uropod peduncle 1.4× medial ramus, 2× lateral ramus, the outer margin with one slightly sub apical distal robust seta and one ventrodistal robust seta, dorsal margin with three robust setae, medial margin with one sub apical robust seta, rami of unequal length—medial 1.4× lateral—without marginal robust setae, both with four apical robust setae; second uropod peduncle slightly longer than rami—1.5× lateral, 1.2× medial—with one short dorsolateral robust seta plus a slightly sub apical robust seta, and one subdistal medial robust seta; rami without marginal robust setae, both with four apical robust setae; third uropod peduncle as long as urosomite three, 0.4× outer ramus, with one medial and one laterofacial robust seta, three distolateral and one distoventral robust seta; proximal article of outer ramus with one mid-medial and two mediodistal robust setae, two lateral and two distolateral robust setae; distal article length 0.27× proximal, with two small apical setules; inner ramus small, 0.1× length outer ramus, with one small apical robust seta. *Telson* (Fig. 12): moderately long, 1.6× urosomite three, longer than broad, length 2.1× width, cleft 12%, apices with a single robust seta set in a notch, single penicillate setules either side at M0.88

Relationship. *Neocrypta robinae* differs from *N. primaris* in: the short length of its antennae, which also have fewer flagellar articles; lacking C but with greater numbers of D and E setae on the mandibular palp; less rugosity of the first gnathopod, and with greater numbers of palmar robust setae on both gnathopods; second article of peraeopods 5–7 less posteriorly expanded; outer rami of pleopods with fewer articles; telson cleft less and narrower. *Neocrypta robinae* differs from *N. simoni* in: first antenna shorter but with a greater number of flagellar articles; second antenna without aesthetascs; mandibular palp bearing many more D and E setae; left first maxilla palp not narrowed; first gnathopod less rugose, both gnathopods with more spinous palms; outer rami of pleopods with more articles; telson less cleft and narrow. *Neocrypta robinae* differs from *N. georginae* in: second antenna flagellum of less articles, and without aesthetascs; mandibular palp with more D and E setae; first gnathopod less rugose and without facial rugosities; outer rami of the pleopods with more articles; uropods are less spinous; telson not tumid, and longer.

Distribution. Diprotodon Cave, Canomodine, New South Wales, 33°30'S 148°52'E.

Neocrypta moniae n.sp.

Figs 13–16

Etymology. Named for the first daughter of the first author in recognition of her indirect support of amphipod research and contributions in field collections.

Type locality. Bowan Park, New South Wales, Cave BP 13, 31°54'S 148°05'E.

Material examined. HOLOTYPE (Australian Museum P51364) female 6.5 mm; collected by S. Eberhard; 13 March, 1995.

Diagnosis. Lateral cephalic lobes weakly projecting, antennal sinus weak, eyes absent, ratio of lengths of peduncular articles of first antenna 10:11:8, ratio of lengths of mandibular palp articles 8:11:13, article 3 almost linear, with DE setae. The inner plate of the first maxilla with two apical plumose setae, inner plate of the second maxilla with one member of the distomedial slightly sub marginal, coxa 1 tapering apically, articles 2–4 of both gnathopods bearing posterior rugose lobes, three robust setae at the palmar corners, robust setae along the palms sparse on first, moderate on the second gnathopod. Peraeopod 6 longer than 7, legs 5–7 moderately lobate post-ventrally on the second article. Outer ramus of pleopods of moderate length, of 9,8,8 articles, inner rami reduced to one article each, without marginal setae. Epimera without postventral teeth, with facial robust setae on some, margins of rami of uropods 1 and 2 with one row of dorsal robust setae only, the lateral ramus of uropod 1 without dorsal robust setae, inner ramus of third uropod reaching to M0.09 of outer. Telson cleft 16%, bearing mid lateral dorsal spination.

Description of holotype (female). *Body* (Fig. 13): pleon with few dorsal arms, pleonites 1–4 with few setae, pleonite 5 with three lateral robust setae, pleonite 6 with one distolateral robust seta, length 5.5 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 13): long, length 0.7× body, 2.4× second antenna, the peduncle shorter than the flagellum, ratio of lengths of articles 23:26:19, setae sparse, flagellum of 22 articles, aesthetascs present on articles 6–22, flagellar segments uniform, sparsely setulate; accessory flagellum 2-articulate, reaching to M0.5 of the second article of the primary flagellum. *Second antenna* (Fig. 13): length 0.3× body,

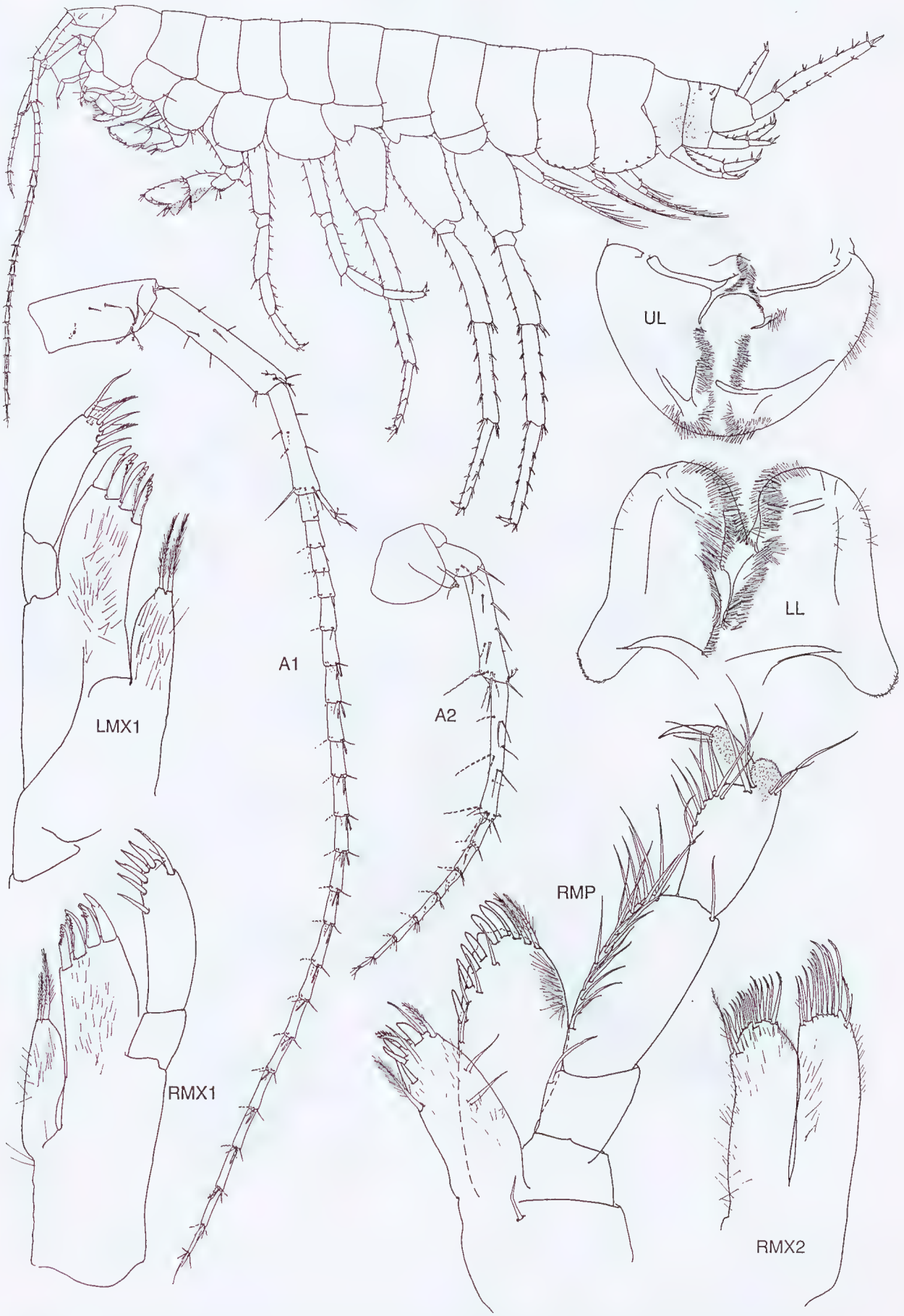

Fig. 13. *Neocrypta moniae* n.sp. holotype female 6.5 mm; whole, antennae, mouthparts.

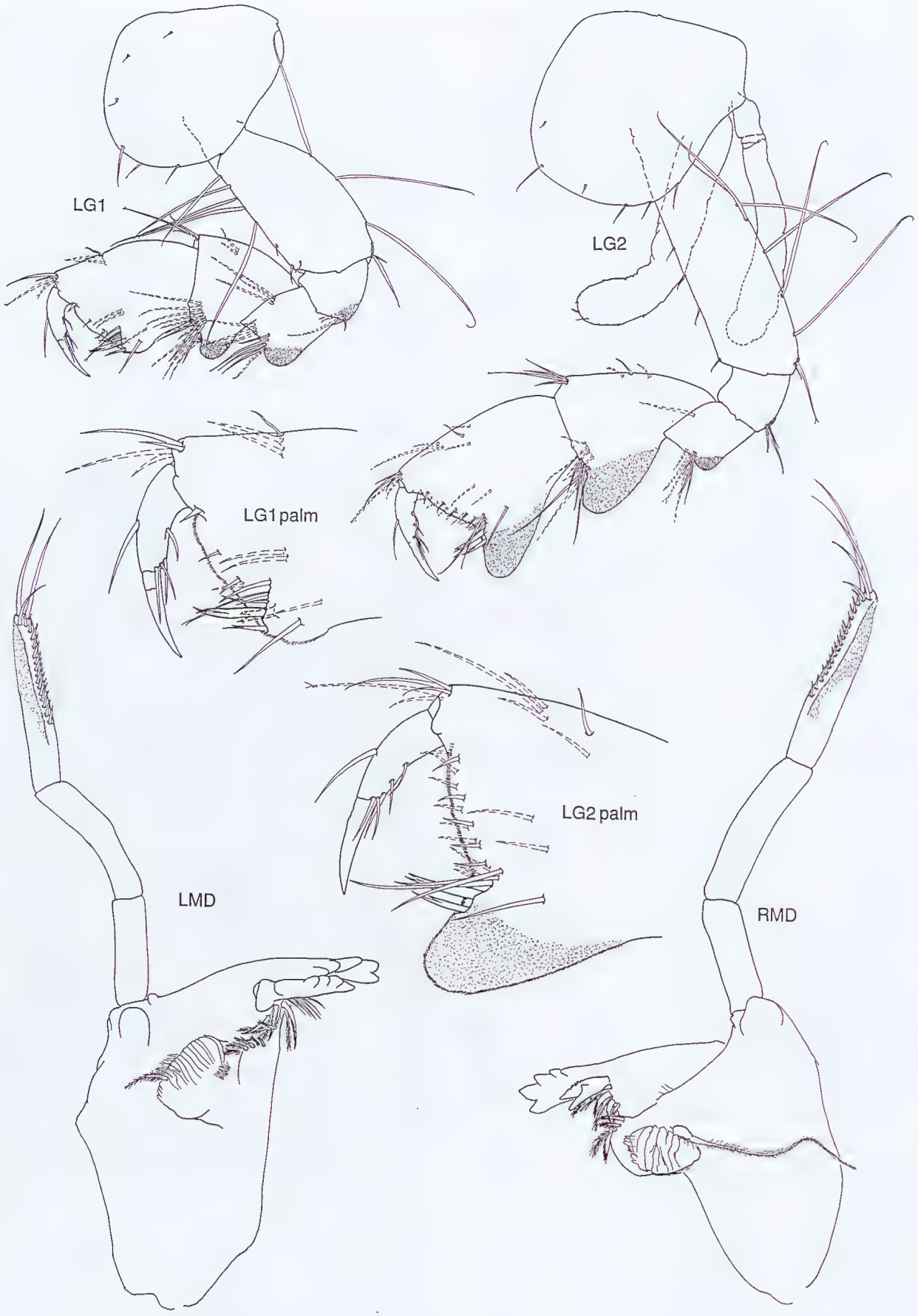

Fig. 14. *Neocrypta moniae* n.sp. holotype female 6.5 mm; mandibles, gnathopods.

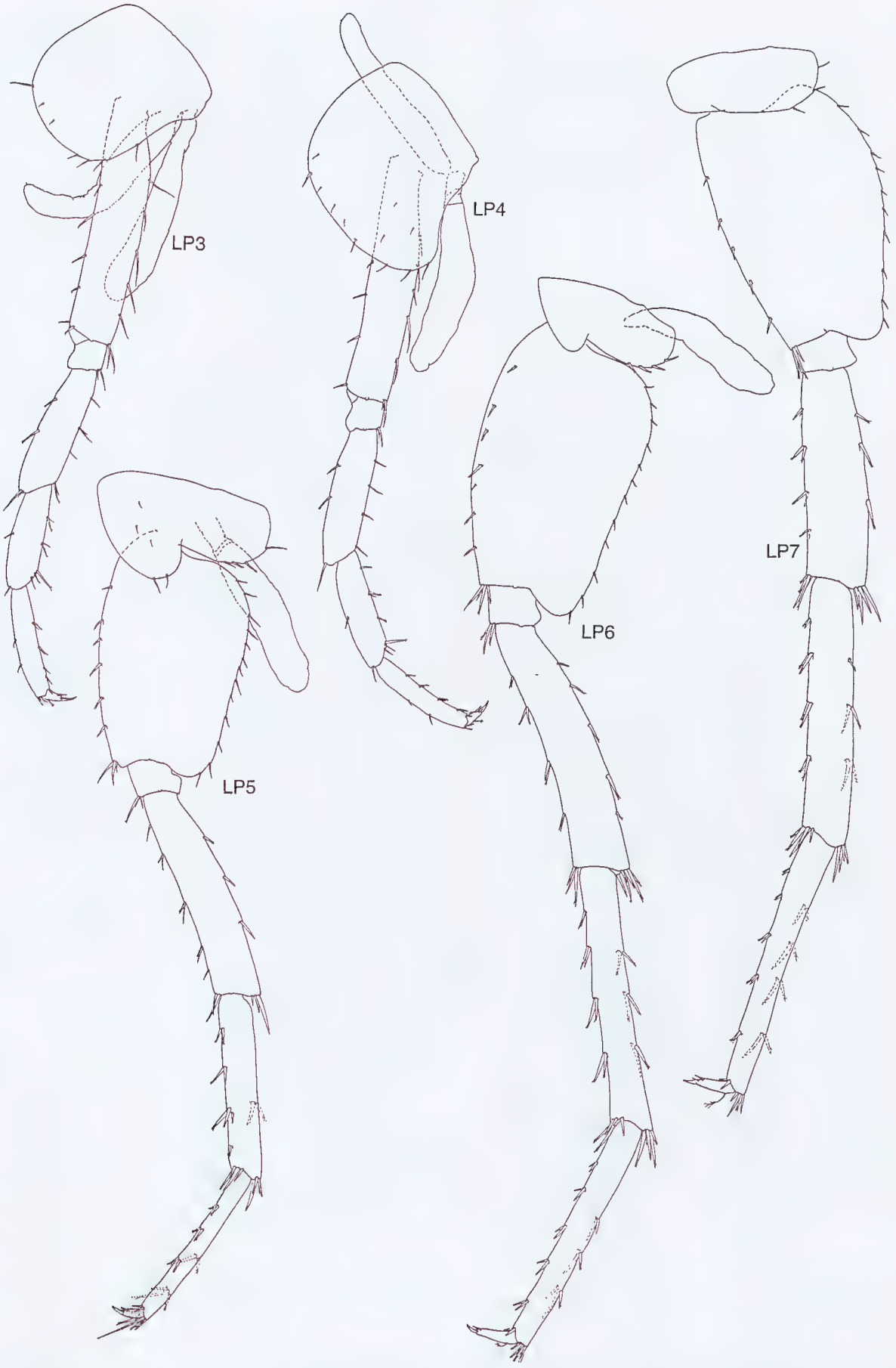

Fig. 15. *Neocrypta moniae* n.sp. holotype female 6.5 mm; peraeopods.

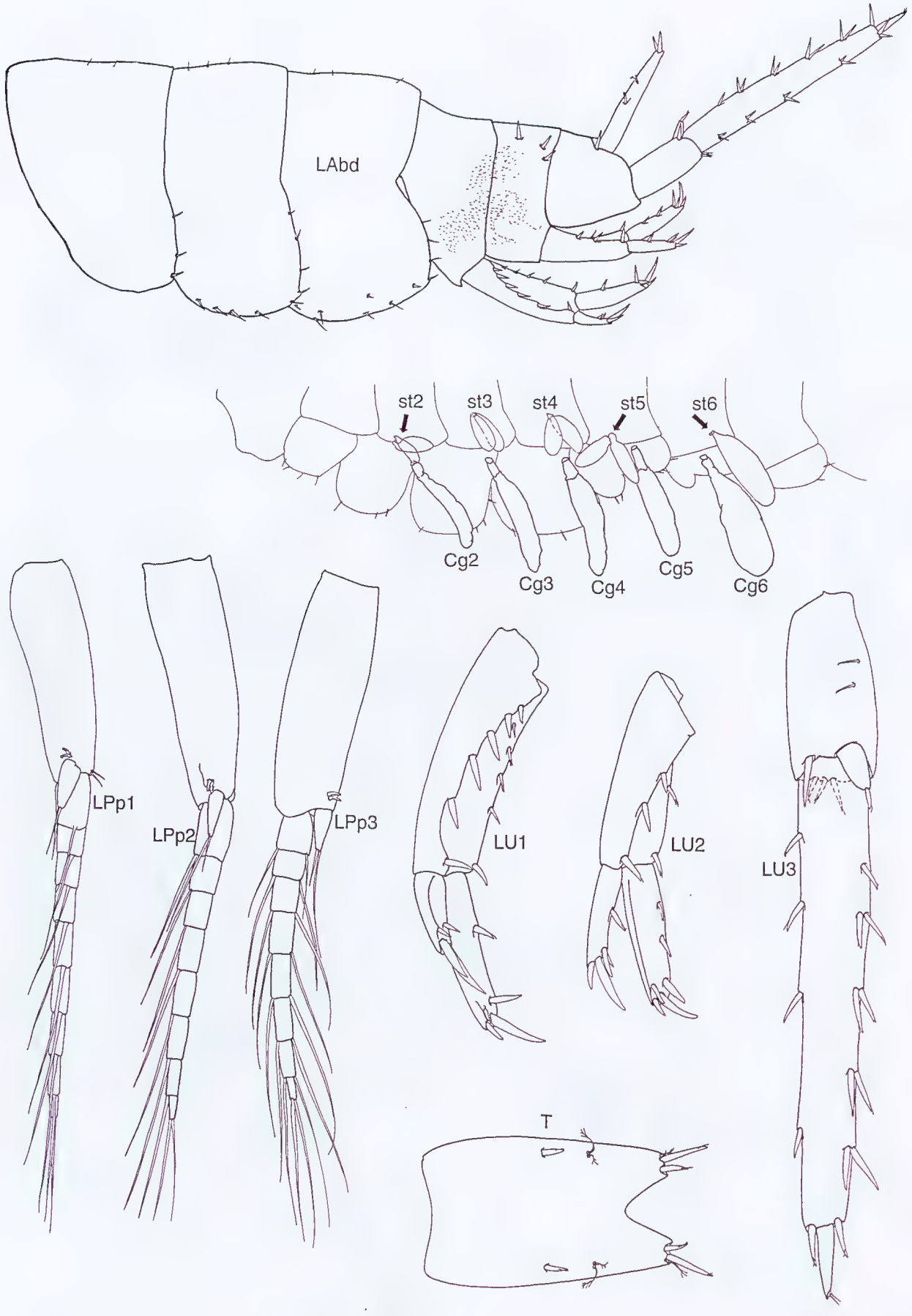

Fig. 16. *Neocrypta moniae* n.sp. holotype female 6.5 mm; abdomen, gills, pleopods, uropods, telson.

peduncle longer than flagellum—1.9×—article 4 slightly shorter than five—21:24—articles 3–5 with moderate ventral setation; flagellum of seven articles, weakly setose ventrally. *Left mandible* (Fig. 14): palp article 3 longer than 2—25:20—linear and distofacially rugose, setae 14D3E; incisor with five teeth, lacinia mobilis four; six slender naked setae basal to the incisor; accessory blades of three rakers and four interraker plumose setae, five brushy setae onto the base of the molar; molar triturative with a short posterior pappose seta. *Right mandible* (Fig. 14): palp article 3 with 15D4E setae, the third article facially rugose; incisor with five teeth; lacinia mobilis bifid, denticulate anteriorly, posteriorly bearing long incisive edge, two slender naked setae and a plumose robust seta basal to the mandible; accessory blades of three rakers, five interraker plumose setae, and a short hooked seta; molar triturative with a long posterior pappose seta. *Maxillae* (Fig. 13). Left first maxilla with two apical and three apicomedial robust setae and one ventrofacial sub apical robust seta; two robust setae naked, the others armed basally or apically with long or short setules; outer plate with seven apically dentate strong robust setae; inner plate two plumose apical setae. Right first maxilla palp article 2 with a row of four stout, mediodistal to distal, apically armed robust setae, one similar apicolateral robust seta and one mediodistal naked robust seta; outer plate with seven denticulate apical robust setae; inner plate with two apical plumose setae. Second maxilla outer plate with two setae on the apicolateral margin; inner plate apicomedial corner with one submarginal thick seta and one plumose seta. *Maxilliped* (Fig. 13): palp article 3 without setae on the inner ventral face, the outer apex with two medial and two lateral setae basal to a strongly produced rugose apical lobe; dactyl with two accessory robust setae basal to the nail, medially rugose; inner plate apex with two thick naked tooth like robust setae, one distal and one apicolateral plumose seta, a slender distal seta, two medial submarginal, and one mid facial setae, with a single naked basal seta; outer plate with a row of six slender naked setae extending from the basomedial face to the mid distal face, a row of seven blunt naked tooth like robust setae from the mid medial margin across the apical face almost to the lateral apex, continuous with a pair of distolateral plumose setae, the distomedial and apical margin broadly scalloped. *Gnathopods* (Fig. 14): coxal plate of the first gnathopod with four short to moderate length apical setae; articles 2–4 with progressively enlarged posterior rugose hump, the fourth forming a strong lobe; carpus short, posteriorly lobate, the lobe rounded, without apical setae and rugose; propodus trapezoidal, slightly longer than wide, the posterior angle rounded, with a small rugose hump, robust setae of the palmar corner one medial and two lateral, the dactylus reaching the corner robust setae, with several accessory spinules along the inner margin, but without a recumbent robust seta. Second gnathopod moderately larger than the first; posterior lobe of the fourth article smaller; carpal lobe larger; propodus with a strong rugose posterior lobe, palmar corner with one medial and two lateral robust setae, dactylus with inner marginal spinules, without recumbent robust seta, reaching robust setae of the palmar corner; coxa bearing slender oostegite and sac like gill, with few short apical setae. *Peraeopods* (Fig. 15): coxa 3 with a sparse apical row of short to moderate setae and single posterior seta; coxa 4 weakly emarginate, with one anteroventral and four postventral setae, several small facial setules and a long oostegite and sac like gill; peraeopods 3 and 4 longer than second gnathopod, subequal, articles 4 and 5 spinous posteriorly, articles 6 with 2-2-1-1 and 2 locking, and 1-2-2-1 and 2 locking robust setae, respectively; peraeopods 5–7 similar; coxae with 4-4-3 robust setae on the ventral margins of the posterior lobes; second articles expanded posteriorly—5>6=7—and moderately lobate, with short posterior setae; propodi of legs 5 and 6 with long setae basal to the dactyls. *Gills* (Fig. 16): coxae 2–6 with sac like gills; sternites 2–6 with simple gills attached to the mid lateral edge. *Epimera* (Fig. 16): without postventral teeth, posterior margins moderately convex with 3-4-4 setae, and 0-5-6 ventrofacial robust setae. *Pleon* (Fig. 16): pleonites 1–4 with few posterior setae; pleonite 5 with three dorsolateral robust setae, six with a single dorsolateral robust seta basal to the telson, pleonites 4 and 5 bearing areas of tiny facial setules. *Urosomite one* (Fig. 16) at the base of uropod 1 bearing a robust seta like extension. *Pleopods* (Fig. 16): two retinacula each; peduncle of pleopod 1 only with two distal setae at the base of the outer ramus; inner rami reduced to a single article each; outer rami with 9,8,8 articles. *Uropods* (Fig. 16): third uropod extending well beyond first and second uropods in the intact specimen; lengths relative to uropod 1—uropod 2 = 0.8×, uropod 3 = 1.6×; first uropod peduncle length 1.7× medial ramus, 3.1× lateral ramus, the outer margin five short robust setae plus a sub apical distal robust seta, medial margin with four robust setae plus an apical robust seta; rami strongly unequal, the medial 1.8× lateral, with reduced spination, only the medial ramus with a single mid medial, short robust seta; both rami with four apical robust setae: second uropod peduncle length 1.4× medial ramus, 2× lateral ramus, with two plus one sub apical lateral robust setae, and one plus one apicomedial robust setae; rami with two medial robust setae on the medial ramus and one lateral robust seta on the lateral ramus, both rami with four apical robust setae; third uropod peduncle length less than the third urosomite—33:38—and 0.36× the length of the outer ramus, with two small basofacial setae, one ventrodistal and a row of three distolateral robust setae; the proximal article of the outer ramus with four approximately evenly distributed lateral robust setae, five transverse medial sets of 1-2-2-2-2 robust setae and single distal lateral and medial robust setae; the second article with a small pair of apical setules; the inner ramus length 0.09× outer ramus, with a single apical robust seta. *Telson* (Fig. 16): moderately long, 1.3× urosomite three, length 1.7× width; cleft 16% with a lateral penicillate setule and two robust setae in small notches dorsal on each lobe, a medio facial robust seta on each side at M0.5, and paired dorsolateral penicillate setules at M0.65 on each side.

Relationship. *Neocrypta moniae* differs from *N. primaris* in: denser medial setae on the maxillipedal palp; denser palmar robust setae; less posterior expansion of the second article of peraeopods 5–7; pleopods with fewer articles of the outer ramus; telson less tumid and shorter. *Neocrypta moniae* differs from *N. robinae* in: longer antennae with more articles; less D and E setae on the mandibular palp; left first maxilla palp broad; maxillipedal palp second article with dense medial setae; greater posterior expansion of the second article of peraeopods 5–7; outer rami of pleopods with more articles; uropods 1 and 2 more spinous; telson more cleft and broader. *Neocrypta moniae* differs from *N. simoni* in: antennal flagellum longer and with more articles; aesthetascs never paired; mandibular palp with many more D setae; left first maxilla palp not narrowed; maxillipedal palp second article with denser medial setation; article 2 of peraeopods 5–7 more expanded posteriorly; outer rami of pleopods with greater numbers of articles; uropods more spinous; telson less cleft, less tumid and more

slender. *Neocrypta moniae* differs from *N. georginae* in: flagellum of first antenna longer, both antennae with more flagellar articles; mandibular palp with more D setae, less E setae; setae of medial margin of maxillipedal palp denser; first gnathopod less rugose; article 2 of peraeopods 5–7 more expanded; pleopod outer rami with more articles; first and second uropods more spinous; telson more cleft, less tumid, more slender.

Distribution. Cave BP13, Bowan Park, New South Wales, 31°54'S 148°05'E.

Neocrypta georginae n.sp.

Figs 17–20

Etymology. Named for the second daughter of the first author in recognition of her indirect support of amphipod studies and assistance in field work.

Type locality. From a pool in the dark zone, Apple Tree Cave, Copperhania, Abercrombie, New South Wales; Cave A 79, 33°55'S 149°22'E.

Material examined. HOLOTYPE (Australian Museum P51365) female "b" 5.5 mm, ALLOTYPE (Australian Museum P51366) male "a" 5 mm, five other small specimens in the type series; collected by S. Eberhard; 16 June, 1995.

Diagnosis. Lateral cephalic lobes moderately projecting, antennal sinus weak, ratio of lengths of peduncles of first antenna 10:10:7, ratio of lengths of mandibular palp articles 8:13:14 to 8:14:15, article 3 weakly falcate, setae DE. Inner plate of first maxillae with two and three apical plumose setae, inner plate of second maxilla without sub marginal medial seta. Coxa 1 apically tapered, articles 2–6 of both gnathopods with posterior rugose projections, three robust setae at corners of palms, length of peraeopod 6 equal to seven, articles 2 of peraeopods 5–7 moderately to weakly lobate. Rami of pleopods reduced, inner rami each of one article without marginal setae. Epimera without postventral teeth and ventrofacial robust setae, spination of the rami of the first and second uropods reduced to a single robust seta for each pair, inner ramus of the third uropod 0.11× length of outer ramus. Telson cleft 11% with only a single mid lateral robust seta on one side.

Description of holotype (female). *Body* (Fig. 17): pereion with few armaments, pleonites 1–4 with sparse short dorsal setae, pleonite 5 with a distal transverse row of three dorsal to dorsolateral robust setae, six with a single mid dorsal robust seta; length 5.5 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 17): moderately long, 0.42× body, 1.7× second, peduncle shorter than flagellum—71: 116,—relative lengths of articles 10:11:7, flagellum of 12 articles, segments uniform, sparsely setulate, aesthetascs present on articles 2–11; accessory flagellum 2-articulate, reaching to M0.3 of the second article of the primary flagellum. *Second antenna* (Fig. 17): length 0.23× body, peduncle longer than flagellum—73:40—article 4 shorter than five—22:26—articles 3–5 with moderate ventral setation; flagellum of six articles, weakly setose ventrally, article 6 with a small apical aesthetasc. *Left mandible* (Fig. 18): palp article 3 subequal to two, ratio of lengths 8:14:15, weakly falcate medially and distally rugose, setae 8D4E, first and second articles naked; incisor with five teeth; lacinia mobilis five teeth and four long basal setules; accessory blades of three chisel robust setae and two plumose robust setae, several fine setules basal to the molar; molar triturative with a short pappose posterior seta. *Right mandible* (Fig. 18): palp article 3 slightly longer than three, ratio of lengths 8:13:14, medially rugose, setae 8D4E, first and second articles naked; incisor with five teeth; lacinia mobilis bifid, denticulate, basally setose; accessory blades two chisel robust setae and two plumose robust setae, two brushy setae basal to molar; molar triturative with a long posterior pappose seta. *Maxillae* (Fig. 17): palp of left first maxilla with five thin apical robust setae and one medial sub apical robust seta; outer plate with seven denticulate strong robust setae; inner plate with two plumose apical setae; right first maxilla with three apical and one medial sub apical thick robust setae, one facial and one ventral simple seta, a long distofacial strong naked seta and distolateral slender robust seta; outer plate with seven denticulate strong robust setae; inner plate with three apical plumose setae; second maxilla with long curved terminal setae, inner distal margin without a submarginal seta. *Maxilliped* (Fig. 17): palp article 3 without ranks of fine setae on the inner basal face; with moderate distomedial setation, a pair of ventrofacial setae basal to the dactyl, without lateral setation, the apex strongly produced and rugose, the dactyl facially rugose with a pair of accessory spinules basal to the nail; article 2 naked laterally with a medial row of long naked setae, outer plate with a row of basomedial simple setae, a distomedial to apical row of six submarginal to facial tooth like robust setae and two distolateral plumose setae, apex of the inner plate with two moderate naked tooth like robust setae and a brushy seta, distolaterally a slender simple seta, two medio facial slender robust setae and a submarginal disto medial short robust seta. *First gnathopod* (Fig. 18): coxal plate with three moderate distal setae, article 2 with three posterior rugose keel like extensions, article 3 with a small posterior rugose hump, article 4 with a distinct posterior rugose lobe; carpus short with a distinct rugose lobe, rounded and without apical setation; propodus with a small posterior rugose keel and a mid dorsofacial area of rugosity, trapezoidal, longer than wide with two lateral and one facial palmar corner robust setae, palm with moderately crowded simple robust setae, dactyl with accessory inner edge spinules, reaching to the palmar corner. *Second gnathopod* (Fig. 18): slightly larger than first, articles 2–4 with small posterior rugose humps; carpus and propodus with strong rugose lobes; carpus short, lobe larger than on gnathopod 1; propodus with a small mid dorsal area of rugosity, palmar corner marked with two lateral and one medial robust seta, palmar robust setae moderately sparse and simple, dactyl with accessory inner margin setules, reaching beyond palmar corner robust setae; coxa sparsely setose apically, bearing a short slender sac like gill and long narrow oostegite. *Peraeopods* (Fig. 19): coxae 3 and 4 weakly setate apically, coxa 4 very weakly emarginate, both bearing slender sac like gills and long slender oostegites; peraeopods 3 and 4 subequal, longer than gnathopod 2, articles 4 and 5 sparsely spinose posteriorly, articles 6 with 1-1-1-1 and 1-1-1-1-1 posterior setae respectively; peraeopods 5–7 similar, 5 shorter than 6 and 7, coxae with 1-1-0 weak posterior robust setae, articles 2 posteriorly expanded, weakly postventrally lobate, with sparse moderate to weak marginal setae; propodi with few posterior setae, but peraeopods 5 and 6 with long basodactylar seta. *Gills* (Fig. 20): coxae 2–6 bearing slender to moderate sac like gills; sternites 2–6 each with a pair of simple gills attached to the mid medial area of each segment. *Epimera* (Fig. 20): without postventral teeth, posterior margins convex, with few moderate setae, the ventral faces with 1-3-4 facial robust setae. *Pleon* (Fig. 20): pleonites 1–4 with sparse dorsal setae; pleonite 5 with a transverse dorsal row

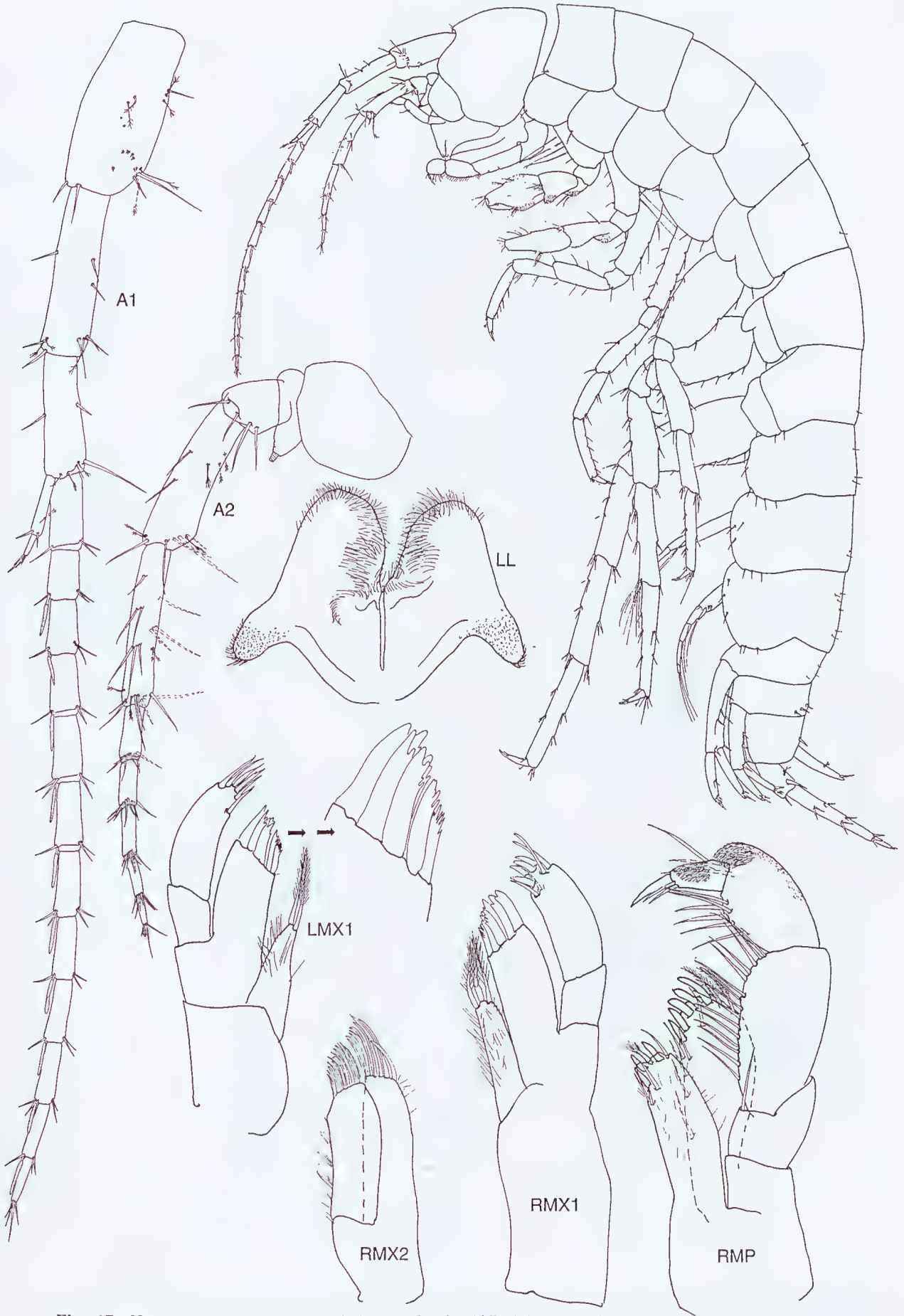

Fig. 17. *Neocrypta georginae* n.sp. holotype female "b" 5.5 mm; whole, antennae, mouthparts.

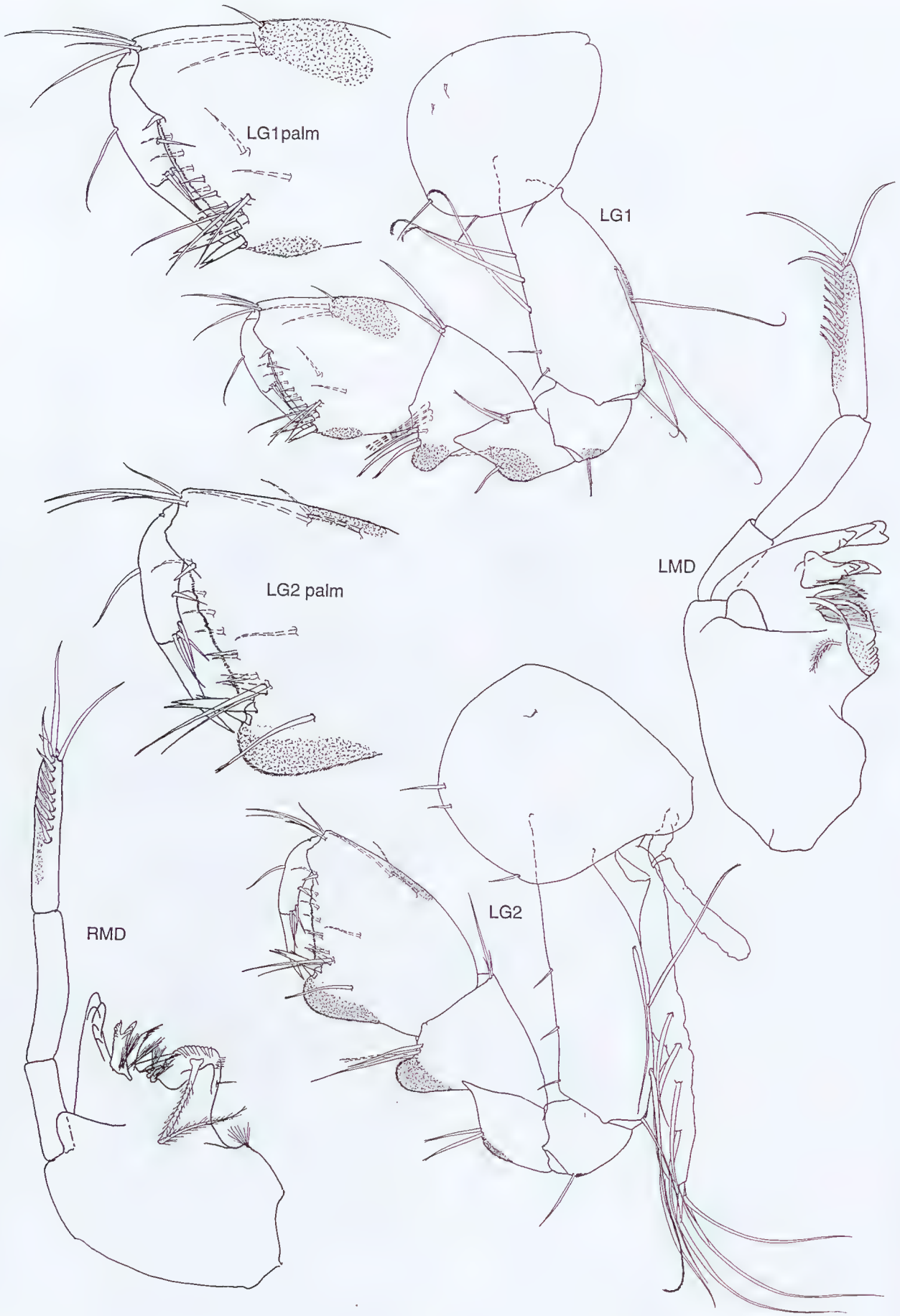

Fig. 18. *Neocrypta georginae* n.sp. holotype female "b" 5.5 mm; mandibles, gnathopods.

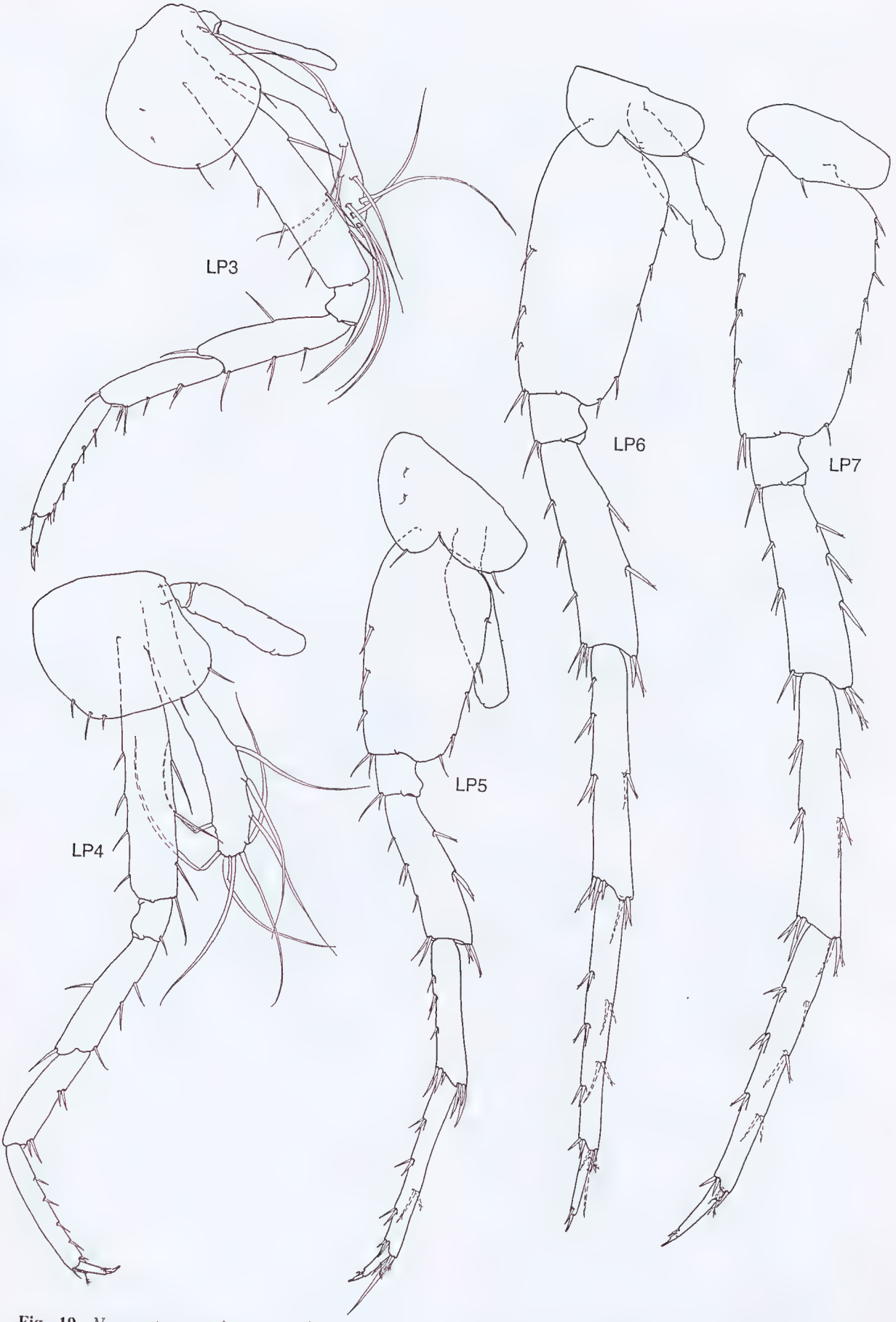

Fig. 19. *Neocrypta georginae* n.sp. holotype female "b" 5.5 mm; peraeopods.

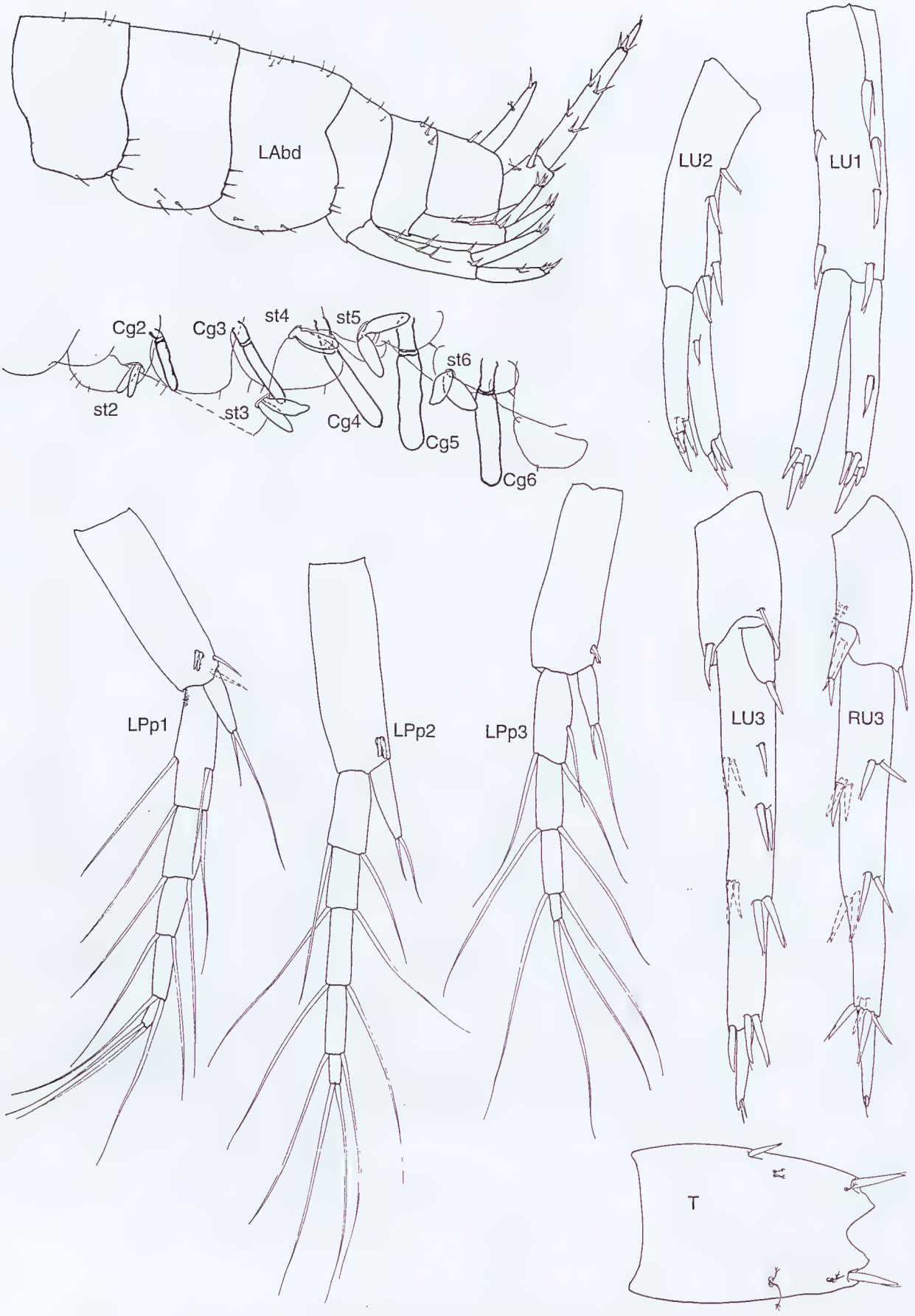

Fig. 20. *Neocrypta georginae* n.sp. holotype female "b" 5.5 mm; abdomen, gills, pleopods, uropods, telson.

of three moderate robust setae; six with a single dorsal robust seta basal to the telson. *Pleopods* (Fig. 20): each with two retinacula; peduncle one with two apicomedial setae, rami strongly reduced, outer rami of 5-5-4 articles, inner rami each of one article, without marginal setae. *Uropods* (Fig. 20): uropod 3 extending beyond 1 and 2 in the intact specimen; lengths relative to uropod 1, uropod 2 0.8×, uropod 3 1.3×; uropod 1 peduncle length 1.3× medial ramus, 1.4× lateral ramus, outer margin with three dorsal robust setae and one subdistal robust seta, inner margin with one dorsal robust seta and one subdistal robust seta; rami of subequal length, inner ramus without marginal robust setae and four apical robust setae, outer ramus with one lateral marginal robust seta and four apical robust setae; second uropod peduncle length 1.2× medial ramus, 1.5× lateral ramus; outer margin with two dorsal robust setae and one subdistal robust seta, inner margin with only a sub apical robust seta; inner ramus with one lateral robust seta and four apical robust setae, outer ramus without marginal robust setae and with four terminal robust setae; uropod 3 peduncle length almost as long as urosomite three, 0.29× outer ramus, the left uropod without facial robust setae on the peduncle, with a moderate dorsal robust seta and a simple seta basal to the inner ramus; outer ramus with transverse rows of 2-2 lateral and 1-2-2 medial robust setae, and one distolateral and two distomedial robust setae basal to the distal article; distal article with two small apical setules; inner ramus 0.11× length of outer ramus, with a single apical robust seta; right third uropod with three small ventrofacial setae, a moderate robust seta adjacent the base of the inner ramus, and one distodorsal robust seta; outer ramus with transverse rows of 2-2 lateral and 3-2 medial robust setae and paired distolateral and distomedial robust setae basal to the distal article; distal article with one small apical seta; inner ramus with a single apical robust seta. *Telson* (Fig. 20): moderately long, as long as urosomite three, length 1.5× width; cleft 11%; apices with one robust seta, the right side with a single penicillate setule, the left with two; a single laterodorsal robust seta on the right side only, at M0.5; paired lateral penicillate setules at M0.6 on either side.

Description of allotype (male "a"). *Body*: length 5 mm. *First antenna*: peduncle sparsely setulate, relative lengths of articles 10:9:7; accessory flagellum of two articles reaching to M0.3 of the second article of the primary flagellum; primary flagellum of 12 articles, all but articles 1 and 12 bearing single aesthetascs. *Second antenna*: peduncle longer than flagellum, relative lengths of articles 4 and 5 27:24; flagellum of four articles, the first relatively long, the last bearing a small apical aesthetasc. *Left mandible*: palp relative lengths of articles 8:13:14, third article rugose, setae 10D3E; incisor with five teeth, lacinia mobilis with four teeth and four fine basal robust setae; accessory blades of two robust setae and two plumose setae, with one large bent brushy seta onto the base of the mandible; mandible triturative, with a short posterior pappose seta. *Right mandible*: palp ratio of lengths of articles 8:14:15, article 2 with one mediodistal seta, setae of third article 8D4E; incisor with five teeth, lacinia mobilis bifid with fine basal and facial setae, accessory blades of two robust setae and two plumose setae; two brushy setae onto the base of the molar; molar triturative with a long posterior pappose seta. *Left first maxilla*: inner plate with two plumose apical setae; outer plate with seven denticulate robust setae; palp with three slender apical robust setae, two distofacial slender setae and two mediodistal slender robust setae. *Right first maxilla*: inner plate with two plumose apical setae; outer plate with seven denticulate robust setae; palp article 2 with a mediodistal to apicolateral row of five moderately broad robust setae, the most lateral armed with setules, and a single distofacial broad naked seta. *Second maxilla*: similar to female except for the presence of two mediodistal plumose setae. *Maxilliped*: inner plate with two broad naked and one moderate plumose apical robust seta, one apicolateral long curved robust seta, one distomedial plumose seta and two distofacial stout robust setae. *Pleopods*: peduncle of each with two retinacula and one mediodistal seta; inner rami of each one article only; outer rami of 6, 5, 4 articles respectively. *Uropod one*: without a basal robust seta on urosomite one; peduncle with three dorsolateral, one apicolateral, one dorsomedial and one apicomedial robust seta; rami with one lateral robust seta each and four apical robust setae. *Uropod 2*: peduncle with two dorsolateral and one apicolateral and apicomedial robust seta; rami without marginal robust setae, each with four apical robust setae. *Uropod 3*: relative lengths of articles; peduncle 28, inner ramus 8, outer ramus proximal article 62, distal article 15; peduncle bearing single lateral and medial distal robust setae and three small dorsofacial setae; inner ramus with one apical robust seta; outer ramus proximal article with transverse rows of 2-2 plus one distal lateral robust setae and 2-2 plus two distal medial robust setae; distal article with two small apical setules. *Telson*: moderately long, length approximately equal to urosomite three; cleft about 11%; lobes slightly tumid basally; one apical robust seta on either lobe; a pair of lateral penicillate setules at M0.6 on either side.

Relationship. *Neocrypta georginae* differs from *N. primaris* in: antennae short, with less flagellar articles; second antenna with an apical aesthetasc; mandibular palp bears less D setae, but more E setae; first gnathopod bearing facial rugosities; posterior expansion of second article of peraeopods 5–7 slight; pleopod outer rami with fewer articles; telson cleft 11%.

Distribution. Apple Tree Cave, cave A79, Copperhania, Abercrombie, New South Wales, 33°55'S 149°22'E.

Neocrypta annae n.sp.

Figs 21–24

Etymology. Named for the wife of the second author in recognition of her years of indirect support of amphipod studies.

Type locality. Cave BP-6, Bowan Park, New South Wales, 31°54'S 148°05'E.

Material examined. HOLOTYPE (Australian Museum P51367) male 4.5 mm; collected by S. Eberhard; 13 March, 1995.

Diagnosis. Lateral cephalic lobes weak, antennal sinus weak, ratio of lengths of peduncular articles of first antenna 10:11:7, ratio of lengths of mandibular palp articles 8:11:13 to 8:14:17, the third palp article weakly falcate, bearing DE setae, the inner plate of the first maxilla with two apical plumose setae, inner plate of the second maxilla with submarginal medial setae. Coxa 1 weakly tapering, second article of gnathopod 1 and second and third articles of gnathopod 2 without posterior rugose lobe, three robust setae at the palmar corners, robust setae along the palms sparse, peraeopod 6 longer than seven, the second articles of legs 5–7 moderately lobate post-ventrally. Rami of pleopods reduced, inner rami of one article only, without marginal setae, epimera without postventral teeth, second and third epimera with ventrofacial robust setae,

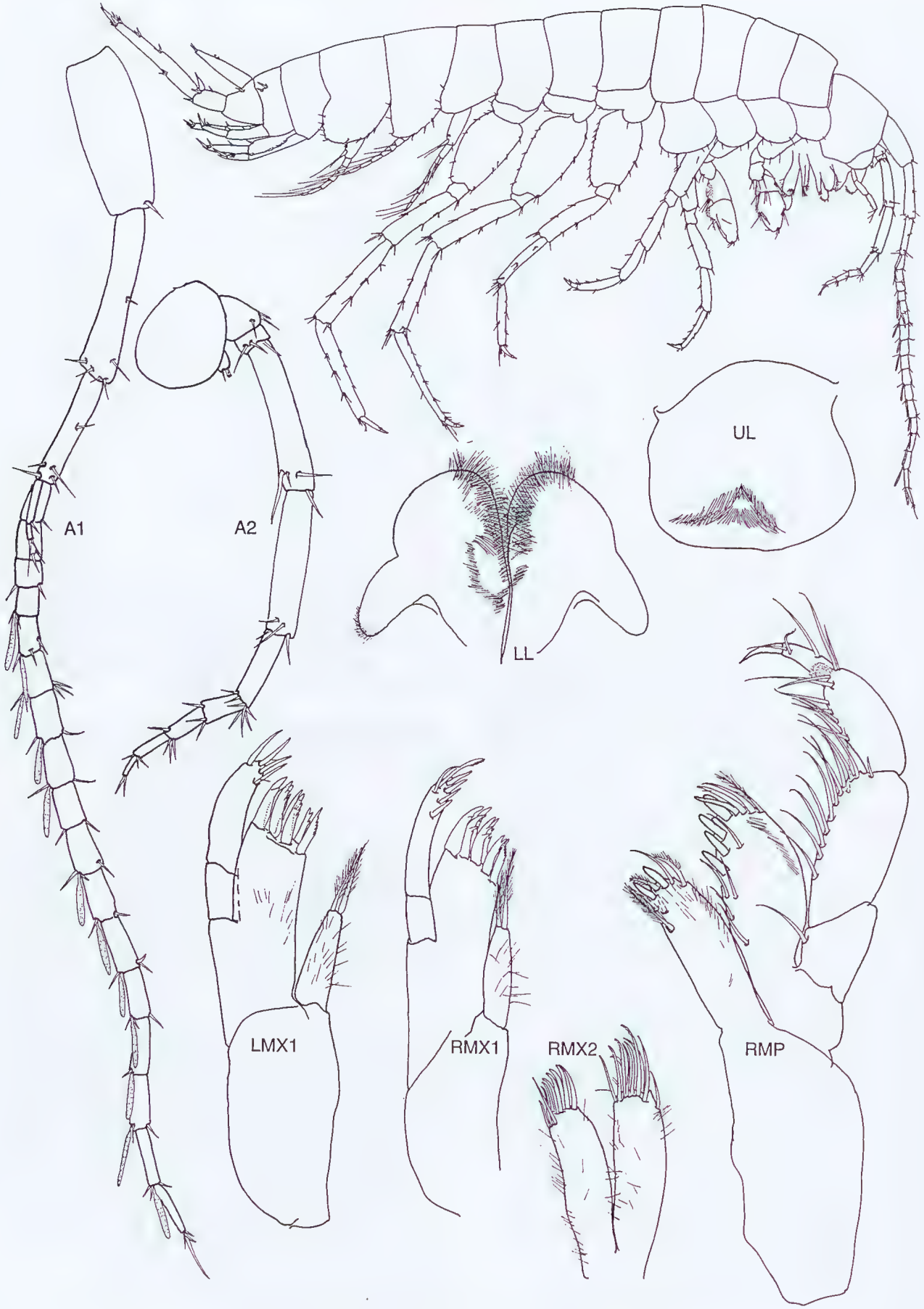

Fig. 21. *Neocrypta annae* n.sp. holotype male 4.5 mm; whole, antennae, mouthparts.

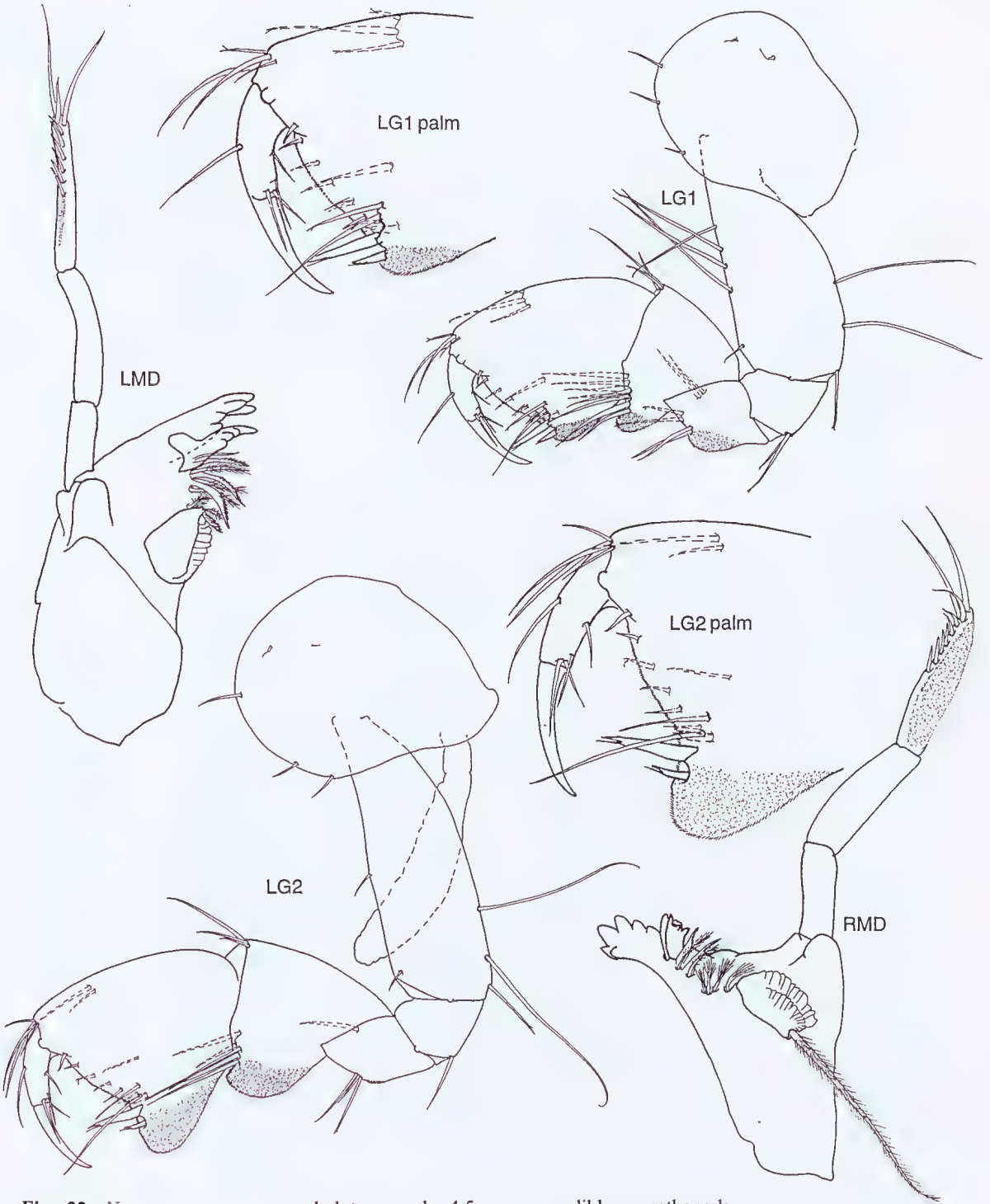

Fig. 22. *Neocrypta annae* n.sp. holotype male 4.5 mm; mandibles, gnathopods.

rami of uropods 1 and 2 with one or no dorsal robust seta rows, the inner ramus of uropod 3 0.09× length of outer ramus. Telson cleft 20%, with mid lateral spination

Description of holotype (male). *Body* (Fig. 21): pleon with few dorsal arms, pleonites 1–4 with few setae, pleonite 5 with two distolateral robust setae, pleonite 6 with one mid dorsolateral robust seta basal to the telson, length 4.5 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 21): length 0.56× body, 2.1× second antenna, peduncle shorter than flagellum; ratio of lengths of peduncular articles 25:27:18, with sparse setae; flagellum of seventeen articles, uniform and sparsely setulate, aesthetascs present on articles 4–17; accessory flagellum 2-articulate, extending to M0.5 of the second primary flagellum article. *Second antenna* (Fig. 21): length: 0.27× body; the peduncle much longer than flagellum—68:35—articles 4 and 5 subequal in length, articles 3–5 with moderate ventral setation; flagellum of five articles, weakly setose ventrally, aesthetascs absent. *Left mandible* (Fig. 22): palp article 3 1.2× article 2, weakly falcate, with setae 6D3E, articles 1 and 2 naked; incisor with five teeth; lacinia mobilis with four; three chisel robust seta accessory blades with three

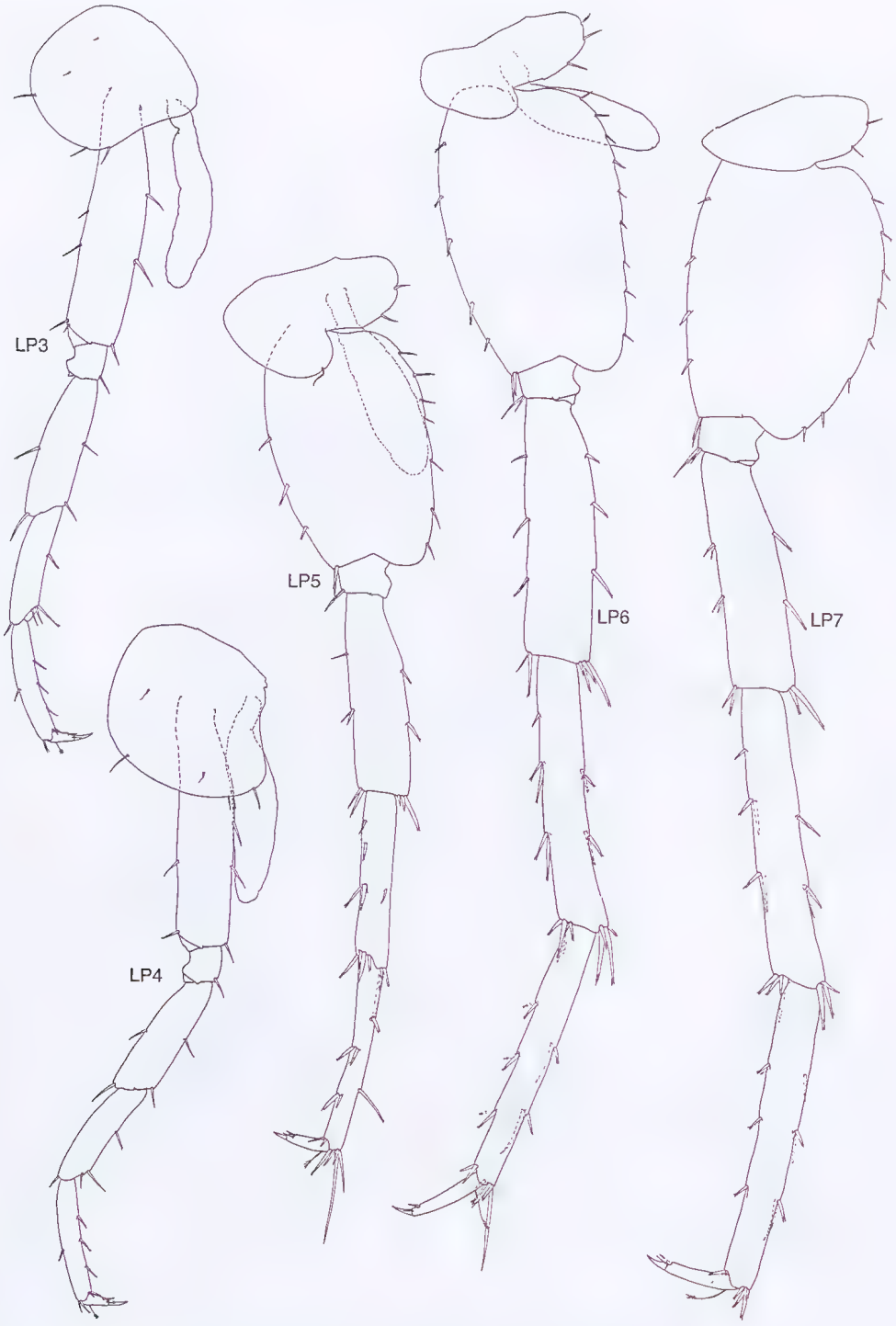

Fig. 23. *Neocrypta annae* n.sp. holotype male 4.5 mm; peraeopods.

interraker plumose setae and one naked robust seta at the base of the incisor, two brushy setae leading to the molar; molar triturative with a short anterior raker blade, no pappose seta. *Right mandible* (Fig. 22): palp with setae 6D3E; incisor with six teeth; lacinia mobilis bifid, denticulate; accessory blades of two chisel robust setae and two plumose setae, four brushy setae basal to the molar; molar triturative with a long posterior pappose seta. *Maxillae* (Fig. 21). Left first maxilla: palp with three thin medio distal to apical robust setae and one similar laterodistal robust seta; outer plate with seven denticulate strong apical robust setae; inner plate with two apical plumose setae. Right first maxilla: palp with a mediodistal row of four robust setae and two distolateral long robust seta setae, the distal with apical armaments; outer plate with seven denticulate robust setae, the inner plate with two plumose apical setae. Second maxilla: both plates with long curved apical setae; outer plate distolateral margin with a single small seta; inner plate with two medio distal submarginal slender setae. *Maxilliped* (Fig. 21): palp article 2 moderately setose medially, article 3 with two slender setae basal to the

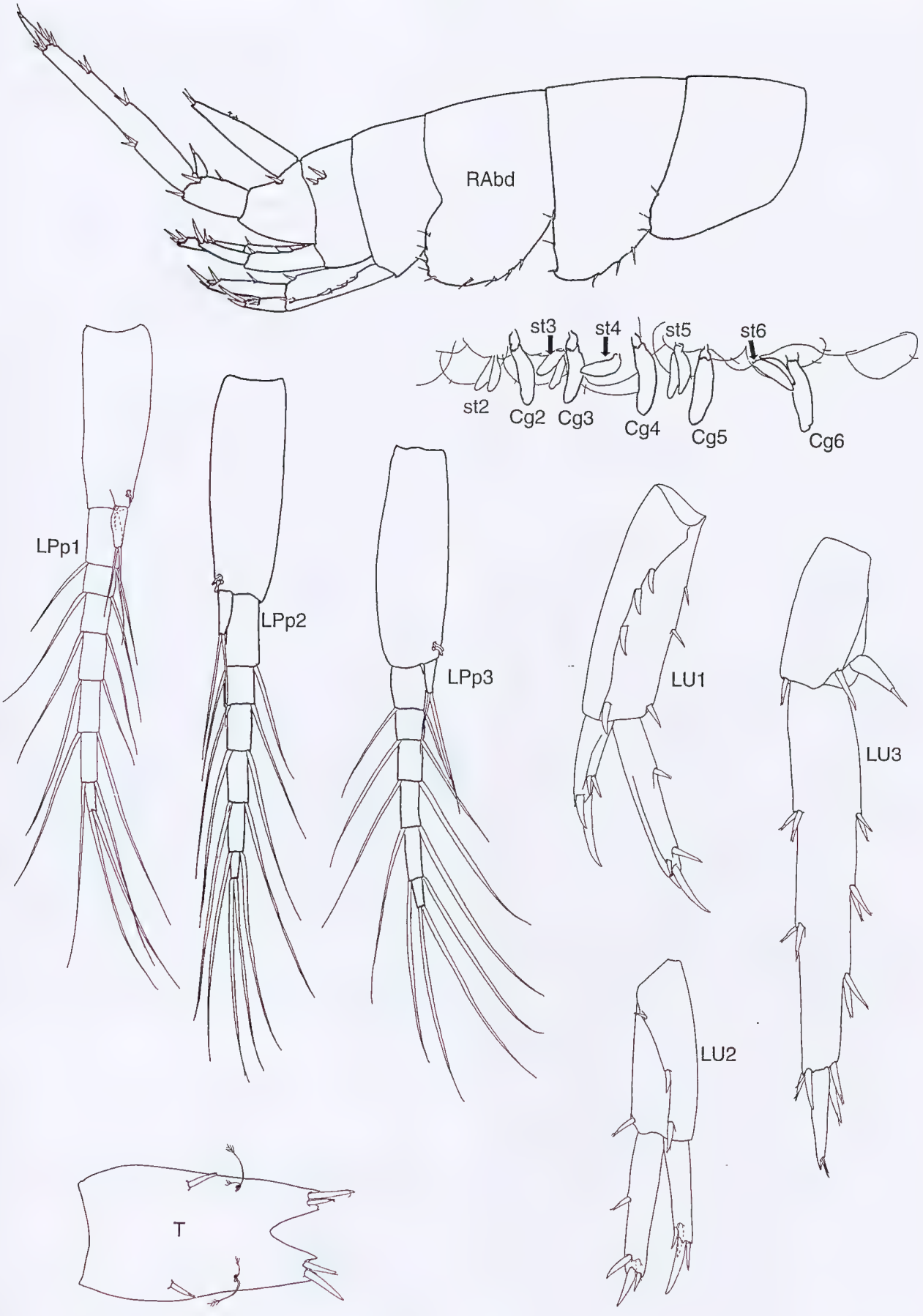

Fig. 24. *Neocrypta annae* n.sp. holotype male 4.5 mm; abdomen, gills, pleopods, uropods, telson.

dactyl, a row of five mediodistal setae, two accessory spinules adjacent the nail, the apex moderately lobate and rugose; inner plate apex with two thick naked robust setae, two plumose and one long naked setae a disto medial plumose seta and two ventrofacial naked setae; outer plate bearing a distolateral plumose robust seta, three slender setae, one naked tooth like robust seta continuous with a row of stout naked sub marginal medial robust setae and a basal row of four slender robust setae. *First gnathopod* (Fig. 22): coxal plate with a row of three moderate length apical setae, article 2 without posterior rugose extension, article 3 with a small postdistal rugose lobe, articles 4–6 with substantial posterior rugose lobes; carpus short, without apical setae on the posterior lobe; propodus trapezoidal, wider than long, posterior rugose lobe keel-like, few, simple palmar robust setae, palmar corner marked by one medial and two lateral robust setae, dactylus with two inner accessory setae and stiff spinules at the inner nail articulation; dactylus reaching slightly beyond the palmar corner robust setae. *Second gnathopod* (Fig. 22): slightly larger than the first; coxa sparsely setose apically, bearing a slender sac like gill; articles 2 and 3 without posterior rugosities; article 4 with only a small mid marginal posterior rugose extension; carpus and propodus strongly lobate; palmar corner with one medial and two lateral stout robust setae, robust setae of palm sparse; dactyl with inner accessory setae, reaching to palmar corner robust setae. *Peraeopods* (Fig. 23): coxae 3 and 4 with three weak apical setae only; coxa 4 weakly emarginate, with a few small facial setules; peraeopods 3 and 4 subequal, slightly longer than the second gnathopod, articles 4 and 5 spinose posteriorly, articles 6 with posterior robust setae 1-1-1 and 1-1-1; peraeopods 5–7 similar, coxae with 2-3-2 weak to moderate posterior robust setae, articles 2 expanded, ovate—P5<6<7—post-ventrally moderately lobate, with small marginal setae, posterior margins of propodi lacking long setae except for long subdactylar setae on legs 5 and 6, dactyls without additional accessory spinules. *Gills* (Fig. 24): coxae 2–6 with sac like gills; sternites 2–6 with paired medial simple gills. *Epimera* (Fig. 24): without postventral teeth; posterior margins of E1 convex, E2 straight, E3 broadly convex, with 3-3-4 posterior setae; ventrofacial robust setae = 0-3-5. *Pleon*: pleonites 1–4 naked, five with two distolateral robust setae, pleonite 6 with one mid lateral robust seta basal to the telson. *Pleopods* (Fig. 24): each with two retinacula, peduncles otherwise naked except for a single small seta basal to the inner ramus of the first pleopod; rami diverse, both reduced, inner rami reduced to a single article only, without marginal setation, outer rami each of six articles. *Uropods* (Fig. 24): third uropod strongly elongate, extending well beyond first and second uropods in the intact specimen; uropod lengths relative to the first uropod 2 0.8×, uropod 3 1.7×. First uropod: peduncle length 1.3× medial, 2.3× lateral rami; apicodistal robust seta of outer margin slightly subapical, with a row of three short dorsal robust setae; medial margin with two robust setae plus the apical robust seta; rami unequal, medial 1.8× lateral, only the medial ramus with a single medial short robust seta, both rami with four terminal robust setae. Second uropod: peduncle longer than rami, 1.2× medial, 1.7× lateral ramus, with two short dorsolateral robust setae plus a distal subapical robust seta; rami unequal, medial ramus 1.4× lateral, only the medial ramus with a single medial robust seta, both rami with four apical robust setae. Third uropod: long, peduncle length 0.9× length of urosomite one, 0.3× length of outer ramus, bearing single distolateral and disto medial robust setae; outer ramus proximal article without setae, with two trans-lateral rows of 2-2 robust setae, three trans-medial rows of 2-2-2 robust setae, three distolateral and two distomedial robust setae, second article short, 0.2× length of the first, with two small apical setules; inner ramus short, 0.09× length of the outer ramus, with a single apical robust seta. *Telson* (Fig. 24): moderately long, 2× urosomite three, 1.8× longer than broad, cleft 20%, apices with one long and one short robust seta, single dorsolateral robust setae at M0.4 on either side and a pair of lateral penicillate setules at M0.6 on either side.

Relationship. *Neocrypta annae* differs from *N. primaris* in: first and second antennae shorter with fewer articles; mandibular palp without C setae, less D and E setae; palp of right first maxilla narrow; first gnathopod more rugose; second article of peraeopods 5–7 less expanded posteriorly; outer rami of pleopods with fewer articles; uropods 1 and 2 with fewer robust setae; telson more deeply cleft, less tumid and narrower. *Neocrypta annae* differs from *N. moniae* in: first and second antennae with less flagellar articles, shorter; mandibular palp with few D setae; palp of right first maxilla narrow; medial margin of article 2 of maxillipedal palp less setose; first gnathopod with little rugosity; outer rami of pleopods with fewer articles; uropods 1 and 2 with fewer robust setae; telson more deeply cleft. *Neocrypta annae* differs from *N. robinae* in: first antenna longer, with more flagellar articles; second antenna longer, but with the same number of articles; mandibular palp bearing fewer D and E setae; palp of right first maxilla narrow; first gnathopod bearing moderate rugosities; second article of peraeopods 5–7 more expanded; telson cleft much more deeply, and broader. *Neocrypta annae* differs from *N. simoni* in: flagellum of first antenna longer and with more articles; second antenna without aesthetascs; mandibular palp with more D setae; right rather than left first maxilla palp narrow; first gnathopod more rugose; outer rami of pleopods of more articles; telson less tumid. *Neocrypta annae* differs from *N. georginae* in: first antenna longer and with a greater number of articles; second antenna with less articles and without apical aesthetasc; mandibular palp with less D setae; palp of right maxilla narrow; first gnathopod without facial rugosities; second article of peraeopods 5–7 more expanded posteriorly; first and second uropods less spinous; telson more deeply cleft, less tumid and more slender.

Distribution. Cave BP6, Bowan Park, New South Wales, 31°54'S 148°05'E.

Neocrypta simoni n.sp.

Figs 25–28

Etymology. Named for the first son of the second author in acknowledgment of his indirect contributions to the study of amphipods.

Type locality. Paradox Cave (Cave J-48), Jenolan, New South Wales, 33°49'S 150°02'E.

Material examined. HOLOTYPE (Australian Museum P51368) female "a" 4 mm, ALLOTYPE (Australian Museum P51369) male "b" 3 mm; collected 9 March, 1993 by S. Eberhard.

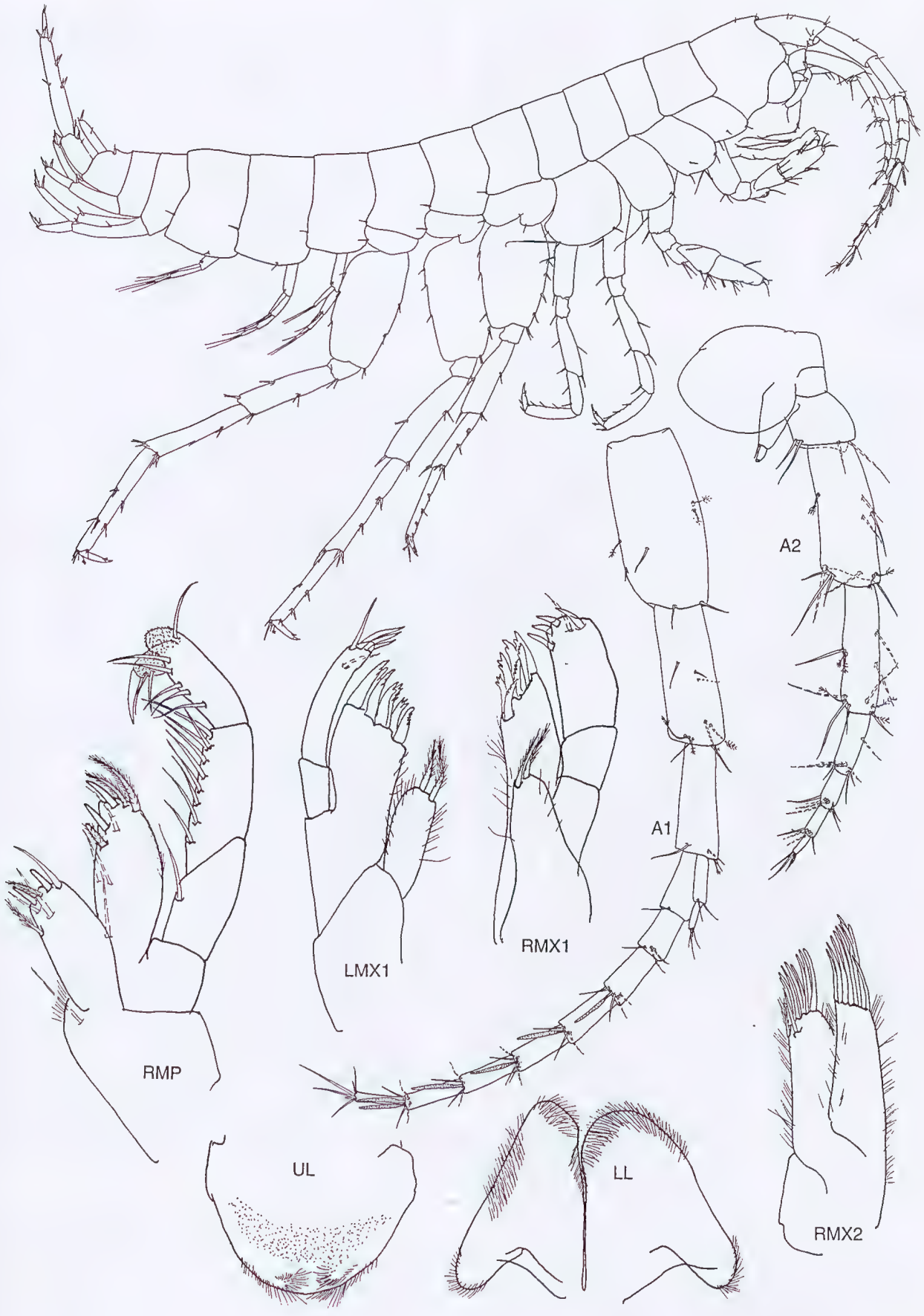

Fig. 25. *Neocrypta simoni* n.sp. holotype female "a" 4.0 mm; whole, antennae, mouthparts.

Diagnosis. Lateral cephalic lobes moderately projecting, antennal sinus moderate, ratio of lengths of peduncular articles of first antenna 10:8:5, ratio of lengths of mandibular palp articles 8:12:10 to 8:13:12, third article linear, setae DE. Inner plate of first maxilla with two plumose apical setae, inner plate of second maxilla with one mediodistal seta submarginal. Coxa 1 tapering apically, articles 2–4 of both gnathopods with posterior rugose lobe, robust setae of the palmar corner 3-2, palmar robust setae short and sparse, peraeopod 6 subequal to seven,, second article of peraeopods 5–7 weakly postventrally lobate. Rami of both pleopods strongly reduced, inner rami of one article only, without marginal setation. Epimera without postventral teeth, rami of pleopods 1 and 2 without dorsal robust seta rows, inner ramus of third uropod 0.13× length of outer ramus. Telson cleft 20%, without mid lateral spination.

Description of holotype (female "a"). *Body* (Fig. 25): pereon and pleon without dorsal armaments except for a single small dorsolateral robust seta on pleonite 6 basal to the telson; length 4 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 25): moderate length, 0.56× body, 1.5× second antenna, peduncle shorter than flagellum, ratio of lengths of articles 10:8:5, setae sparse; flagellum of eight articles, segments uniform, sparsely setulate, bearing single aesthetascs on articles 3–6 and a pair on article 7; accessory flagellum of two articles reaching to M0.2 of article 2 of the primary flagellum. *Second antenna* (Fig. 25): length 0.4× body, peduncle much longer than flagellum—80:30—articles 4 and 5 subequal in length—27:24—articles 3–5 with moderate ventral setation; flagellum 4-articulate, weakly setose bearing a single small apical aesthetasc on article 4. *Left mandible* (Fig. 26): palp article 3 shorter than 2—23:26—linear, with 3D4E setae, distolaterally rugose, articles 1 and 2 naked; incisor with six teeth; lacinia mobilis four teeth; accessory blades of three chisel robust setae and two plumose robust setae; molar triturative with a short posterior pappose seta. *Right mandible* (Fig. 26): palp article 3 setae 3D4E, distolaterally rugose; incisor with five teeth; lacinia mobilis bifid, denticulate; no accessory robust setae, but three very short setae onto the base of the molar; molar bearing a hooked brushy basal seta and long posterior pappose seta. *Maxillae* (Fig. 25): palp of left first maxilla slender, bearing four thin apical robust setae and a ventrofacial seta, outer plate with seven denticulate robust setae, inner plate with two apical plumose setae; right first maxilla palp broad, with four thick mediodistal to apical robust setae and one ventrofacial seta; outer plate with seven strong denticulate robust setae, inner plate with two plumose apical setae; second maxillae: both plates with long curved apical setae; inner plate bearing one subdistal medial plumose seta and one simple disto facial submarginal seta. *Maxilliped* (Fig. 25): palp article 3 without thin basomedial setae, with two facial setae basal to the dactyl, and a single distolateral seta at the base of the strongly produced rugose apex; dactyl facially rugose, with two accessory setules on the inner distal margin; inner plate apex with two thick tooth like robust setae, one pappose robust seta and a long lateral seta, inner margin with one plumose seta, ventrodistal face with two simple setae; outer plate with three naked basofacial setae, medial submarginal pappose and naked robust setae, a ventrofacial long seta, one naked and two long pappose robust setae apically. *First gnathopod* (Fig. 26): coxal plate with two marginal and one ventrofacial setae; articles 2 and 3 with small posterior rugose lobes; articles 4 and 5 with strong posterior rugose lobes; article 6 with a small area of posterior rugosity; carpus short, rugose lobe rounded, without apical setae; propodus trapezoidal, longer than wide, the posterior angle subquadrate, palmar corner robust setae two lateral and one medial, palm with moderate numbers of simple setae, dactyl with recumbent inner tooth like robust seta, and reaching to the palmar corner. *Second gnathopod* (Fig. 26): slightly larger than the first; articles 2–4 all with posterior rugosities; article 4 posteriorly lobate, but less so than on the first gnathopod; carpal lobe larger than on the first; posterior proposal margin strongly lobate and rugose; palmar corner marked with one medial and one lateral robust seta; dactyl with an inner accessory setule, and reaching beyond the robust setae of the palmar corner; coxa sparsely setose apically with a sac like gill and slender oostegite. *Peraeopods* (Fig. 27): coxae 3 and 4 with sparse apical setation, coxa 4 moderately emarginate, both bearing slender sac like gill and oostegite; peraeopods 3 and 4 subequal, longer than gnathopod 2, articles 3 and 4 weakly setose and spinose, both propodi with the posterior robust seta formula 1-1-1-1; peraeopods 5–7 similar, coxae each with only a single weak posterior robust seta, article 2 expanded posteriorly, weakly lobate, with few moderate marginal setae, propodi with few posterior setae. *Gills* (Fig. 28): sac like simple gills present on coxae 2–6; sternites 2–6 bearing paired simple non-dendritic gills on each segment. *Epimera* (Fig. 28): without post-ventral teeth, posterior margins almost straight, each with a single seta only, and single mid ventrofacial robust setae on epimera two and three. *Pleon* (Fig. 28): pleonites 1–5 naked; six with a single dorsolateral robust seta basal to the telson. *Pleopods* (Fig. 28): each with two retinaculae; peduncles without setae or robust setae; rami reduced, outer rami each with three articles, the third outer ramus with a single additional distal seta on the first article; inner rami of one article each, without marginal setae. *Uropods* (Fig. 28): uropod 3 strongly extended, well beyond uropods 1 and 2 in the intact specimen; uropod lengths relative to uropod 1: uropod 2 0.78×, uropod 3 1.3×. First uropod: peduncle length 1.3× medial, and 1.5× lateral ramus, outer margin with a row of two short dorsal robust setae plus a sub apical distal robust seta, medial margin with a sub apical robust seta only; both rami without marginal robust setae, each with four apical robust setae. Second uropod: peduncle 1.3× medial, 1.5× lateral ramus, outer and inner margins with one sub apical distal robust seta; rami without marginal robust setae, each with four apical robust setae. Third uropod: peduncle length 0.35× outer ramus, as long as urosomite three with one small facial seta, a mediodistal robust seta adjacent the base of the inner ramus, and distolateral robust seta; outer ramus proximal article with two transverse medial rows of two robust setae each, two transverse lateral rows of one and two robust setae, and two medial and one lateral distal robust setae basal to the distal article; distal article length 0.26× proximal, with two fine apical setules; inner ramus small, 0.13× outer ramus with a single apical robust seta. *Telson* (Fig. 28): moderately long, longer than urosomite three, length 1.3× width; cleft 20%; apices each with a single robust seta set in a small notch, and a single lateral penicillate setule; without other dorsal spination or setation except for a pair of penicillate setules on either side at M0.49.

Description of allotype (male "b"). *Body*: length 3.5 mm. *First antenna*: primary flagellum of eight articles, aesthetascs present on articles 3–8, those on articles 3 and 4 paired; accessory flagellum of two articles, reaching to M0.4 of the second article of the primary flagellum. *Second antenna*: flagellum of four articles, the fourth with a small apical aesthetasc. *Mandibles*: similar to female. *Gnathopods*: similar to female. *Peraeopods*: leg three second article lacking one long posterior seta, similarly article 5 with one less posterior

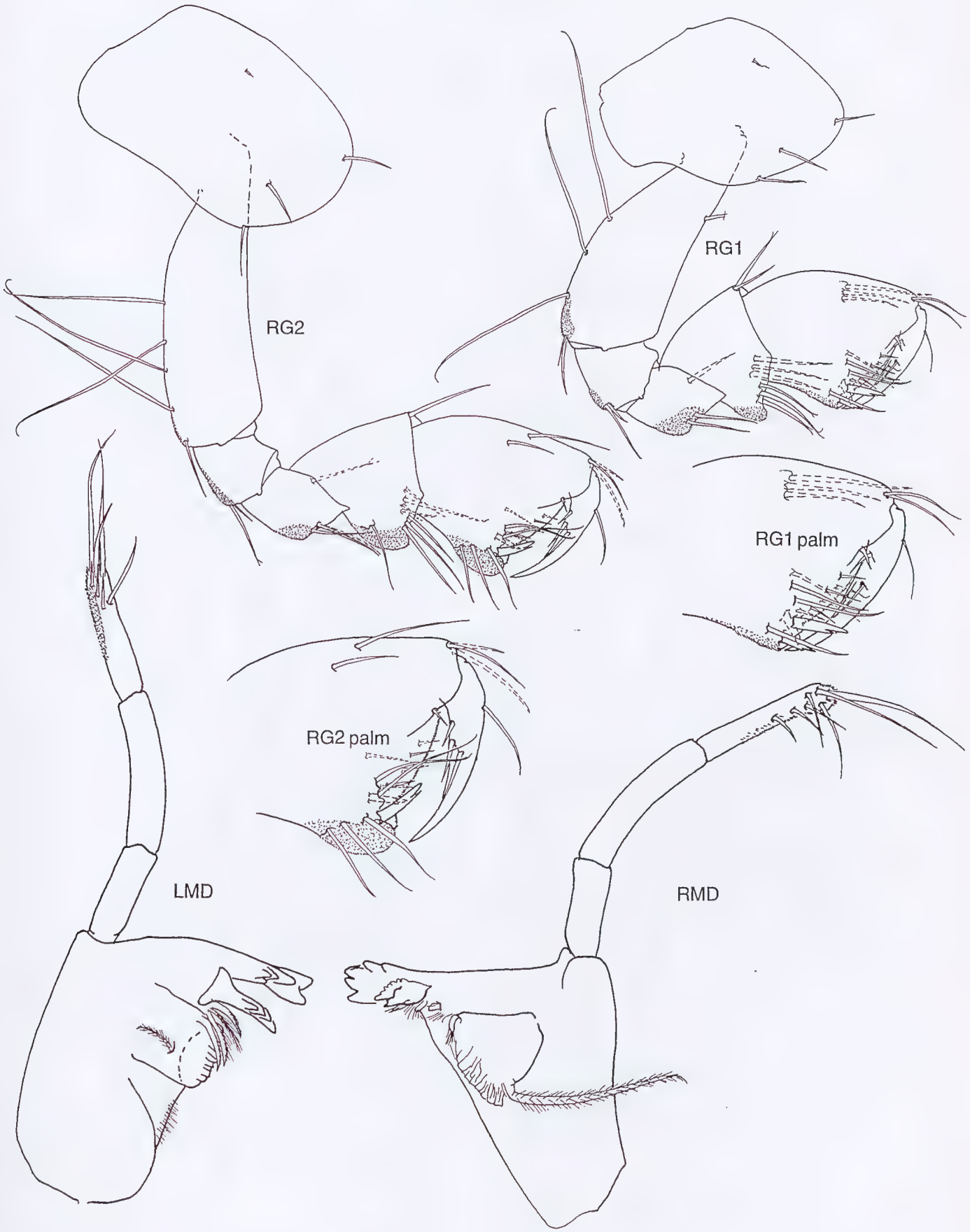

Fig. 26. *Neocrypta simoni* n.sp. holotype female "a" 4.0 mm; mandibles, gnathopods.

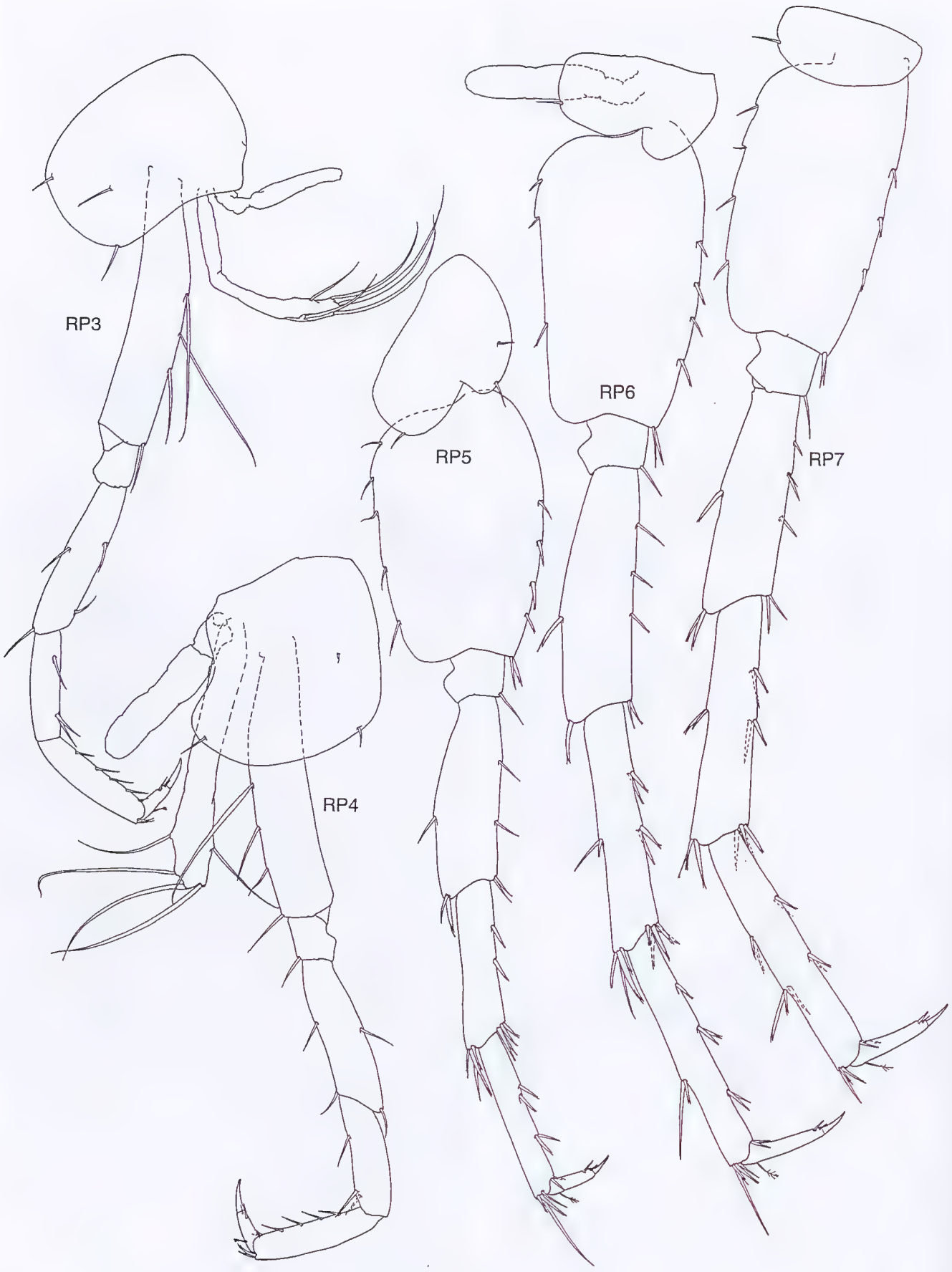

Fig. 27. *Neocrypta simoni* n.sp. holotype female "a" 4.0 mm; peraeopods.

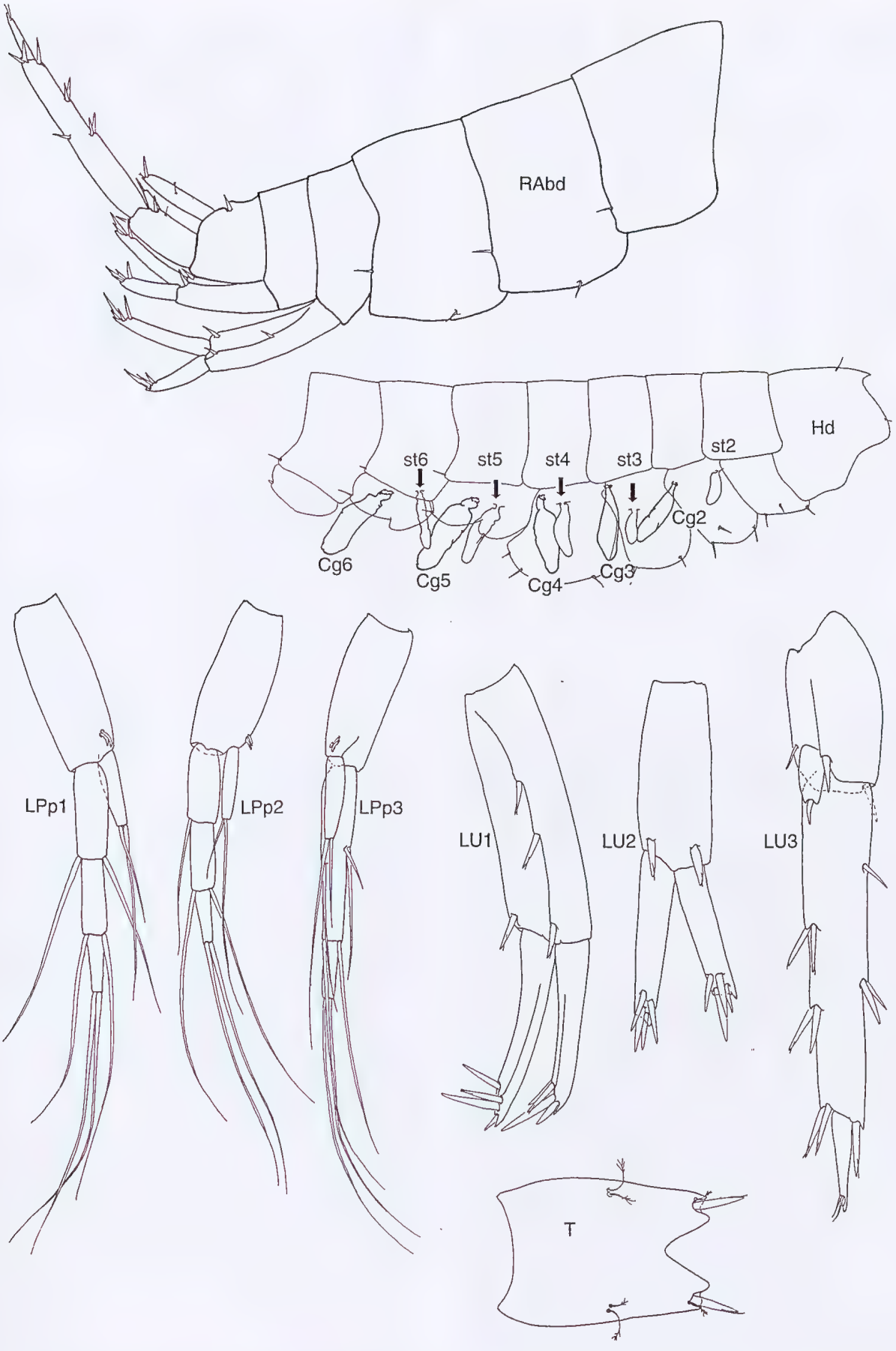

Fig. 28. *Neocrypta simoni* n.sp. holotype female "a" 4.0 mm; abdomen, gills, pleopods, uropods, telson.

seta; other peraeopods also less setose than female. *Pleopods*: similar to female, peduncles each with two retinacula, outer rami with 3-3-2 articles, inner rami each with one article. *Uropods*: first uropod peduncle with one lateral robust seta only; second uropod similarly naked; third uropod peduncle similar to female, outer ramus proximal article with only one lateral robust seta. *Telson*: similar to female.

Relationship. *Neocrypta simoni* differs from *N. primus* in: antennae shorter with few flagellar articles; second antenna bearing apical aesthetasc; mandibular palp with less D setae; left first maxilla palp narrow; article 2 of peraeopods 5–7 less broadly expanded; outer rami of pleopods with fewer articles; uropods 1 and 2 with fewer robust setae; telson cleft more deeply. *Neocrypta simoni* differs from *N. georginae* in: first antenna longest but with fewer articles, some aesthetascs paired; second antenna shorter, with aesthetasc on last article; mandibular palp with fewer D setae; palp of left first maxilla narrow; first gnathopod without facial rugosities; outer rami of pleopods with fewer articles; uropods less spinous; telson cleft more deeply.

Distribution. Paradox Cave (J48), Jenolan, New South Wales, 33°49'S 150°02'E.

Wombeyanus n.gen.

Etymology. Name refers to the type locality: Wombeyan Cave, New South Wales.

Type species. *Wombeyanus botulosus* n.sp.

Diagnosis. Pleonites with weak dorsal arms, rostrum small, lateral cephalic lobes weakly projecting, antennal sinus weak, without eyes. First antenna elongate, longer than the second, the ratio of peduncular articles 10:8:5, the accessory flagellum 2-articulate, calceoli present. The flagellum of the second antenna shorter than the peduncle, with prominent calceoli present. The ratio of lengths of articles of the mandibular palp equals 8:20:20 on the left mandible, 8:15:16 on the right, the second article poorly setose, the third weakly falcate, setae of the third article are BCDE. The labium lacks inner lobes. Inner plates of the maxillae are not setose medially, the first maxilla inner plate ovatotriangular with two apical plumose setae, the outer plate with seven terminal robust setae, the palps asymmetric. The second maxilla lacks an oblique row of facial setae but the two most medial setae of the inner plate are slightly sub marginal. The third article of the maxillipedal palp bears an extended rugose apical lobe. Coxae 1–4 moderately elongate, sparsely setose ventrally, coxae 1–3 without posterior robust setae, coxa 1 weakly tapering apically, coxa 4 moderately emarginate, coxae 5–7 much shorter than coxa 4. Gnathopods small, without sexual dimorphism, carpi short, with a strong posterior rugose lobe, articles 2–4 also bearing rugosities on the post-distal corner, palms transverse to slightly oblique, rugose post-distally, palmar robust setae not bifid nor dense nor bearing triggers, robust setae at palmar corner three or four. Peraeopods 3 and 4 with robust seta sets on the posterior of article 6 evenly spaced, peraeopods 5–7 moderately elongate, six longer than seven, article 2 of peraeopods 5–7 broadly expanded, least on six, ovate, and post-ventrally lobate, articles 4 with few setae, except for an elongate basodactylar seta on peraeopod 5, the anterior margins of article 6 with 5-6-5 robust seta sets as well as locking robust setae. Dactyls of peraeopods with one marginal and one facial setule. Gills present on coxae 2–6, absent from coxa 7. Sternal gills present on segments 2–6, simple sausage like, attached to the antero- or mid-lateral edge of each segment. Pleopods similar; each with two retinaculae, without accessory retinaculae; the rami subequal, medial setae of the inner ramus of each bifid. Epimera without posterior teeth; ventrofacial robust setae present on epimera two and three; the posterior margins with few setae. Robust setae of uropods 1 and 2 all short. Peduncles of uropods 1 and 2 with a single robust seta on the apico medial corner, the rami extending unequally, margins with few robust setae or setae, basofacial arms of the first uropod absent, the third uropod strongly extended, parviramous, the peduncle relatively short, robust setae of the outer ramus arranged in multiples in lateral and medial rows, the outer ramus with two articles, the second short, medial setae absent from the first article, without plumose setae , the inner ramus very short, with two apical robust setae. The telson short, cleft about 46%, the lobes not laterally tumid, with only apical spination, and a pair of lateral penicillate setules at M0.75

Additional description. Upper lip uniform, rounded but weakly asymmetrical below, mandible accessory blades (rakers) with interraker plumose setae, few additional penicillate setae beyond rakers riding onto the base of the molar, with two bent basal molarial ragged setae. The lower lip uniform, the inner lobes absent. Both plates of the second maxilla with long apical setae. Maxilla inner plates and the lateral margins of the second maxilla moderately pubescent. Maxillipedal inner plate with a distal row of a few plumose setae, three blunt naked robust setae, reduced medial row of plumose setae, the outer plate with a few distal plumose setae, continuous with a mediodistal row of blunt naked tooth like robust setae, palp articles 2 and 3 poorly setose laterally, well setose medially, article 3 with several long robust setae near the base of the dactyl. Dactyls of gnathopods without a recumbent inner tooth like robust seta, with stiff spinules or setules at the inner nail articulation, and without additional spinules along the inner dactylar margin. Gnathopod 1 without an enlarged rastellate seta on the fourth article. Pleopods similar, the peduncles with few or no setae, and rami extending subequally. Urosomite one at the base of the first uropod with a moderate ventrodistal robust seta.

Sexual attributes. Oostegites moderately broad, calceoli absent on female antennae. Sexual differences in appendages minor.

Relationship. The genus is most similar to *Neoniphargus*, but differs from that genus in lacking eyes, the first antenna is only moderately longer than the second, the first article of the mandibular palp is relatively longer, there are fewer robust setae at the palmar corners, robust setae along the palm are not dense nor bearing triggers, posterior expansion of the second article is least on peraeopod 6 rather than five, sternal gills are neither dendritic nor bearing lumps, marginal spination of the rami of the first and second uropods is reduced, the telson is cleft 46% rather than 60%, and the lateral penicillate setules are placed more posteriorly, the ventrodistal robust seta on the first urosomite at the base of the first uropod is moderately long rather than short, and in the female is paired on the right side. The genus differs from *Wesniphargus* in the absence of lumps on

sternal gills, presence of rugosities on the propodi of both gnathopods, lack of coxal gill 7, and asymmetry of the palps of the first maxillae. *Wombeyanus* differs from *Tasniphargus* in the absence of long, dense setae or cojoint first articles on the first antenna, as well as absence of dendricity of the sternal gills. *Wombeyanus* differs from *Yulia* in the lack of dense setae on the pleopod peduncles and absence of an elongate spur on the outer ramus of the first uropod of the male, as well as the absence of dendritic sternal gills. *Wombeyanus* differs from *Neocrypta* in the presence of calceoli on the flagellum of the second antenna; the first article of the mandibular palp is relatively short, the second slightly setose, the third bears B and C setae; coxa 4 is moderately rather than weakly emarginate; pleopods are not reduced, inner and outer rami being subequal; telson is short rather than long, and cleft 46% rather than 20% or less.

Wombeyanus botulosus n.sp.

Figs 29–32

Etymology. From Latin *botulosus*, meaning sausage; name refers to the simple, sausage-like sternal gills.

Type locality. Bullio Cave (2W2) part of the Wombeyan Cave system, New South Wales, 34°19'S 149°59'E.

Material examined. HOLOTYPE (Australian Museum P51370) male "x" 7.5 mm, ALLOTYPE (Australian Museum P51371) female "y" 7.5 mm, other in the type series; male 7.5 mm; collected by T. Dennis 5 April, 1986.

Diagnosis. As in the genus.

Description of holotype (male "x"). *Body* (Fig. 29): pleon not armed dorsally, pleonites 1-4 with few setae, pleonites 5 and 6 with one robust seta on each side, length 7.5 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 29): long, 0.55× body length, 1.9× the second antenna; the peduncle length less than the flagellum, the ratio of lengths 10:8:5, setae sparse, the third article bearing a single medial calceolus at M0.7; flagellum of 26 uniform, sparsely setulate articles, calceoli present on articles 2, 4, 5, 7 and 9, and aesthetascs on articles 3–26 excepting articles 8 and 25; accessory flagellum of two articles, extending to M0.7 of the second article of the primary flagellum. *Second antenna* (Fig. 29): length about 0.3× body, peduncle approximately 1.9× the length of the flagellum, peduncular articles 4–5 subequal in length, articles 3–5 bearing moderate ventral setation; flagellum of ten weakly setate articles of which articles 1–7 bear calceoli, the distal three with a single aesthetasc each. *Left mandible* (Fig. 31): palp articles 2 and 3 equal in length, article 2 with four inner marginal setae, article 3 weakly falcate, bearing 2B5C23D3E setae; incisor with five teeth; lacinia mobilis with four teeth and a few fine basofacial setae; three chisel robust seta accessory blades and three interraker plumose setae; molar bearing a moderate posterior pappose seta as well as two brushy and one naked basal setae. *Right mandible* (Fig. 31): palp articles 2 and 3 equal in length, article 2 bearing four medial setae, setae of article 3 2B6C23D3E; incisor bearing five teeth; lacinia mobilis bifid and denticulate with a few medial setules; accessory blades of two blunt chisel robust setae bearing distal rugosities, two bent brushy setae onto the base of the molar; molar barely triturative, bearing a long pappose posterior seta, and a few mediobasal setules. *Maxillae* (Fig. 29): left first maxilla; palp article 2 with a row of four apicomedial and apical slender robust setae, three facial robust setae and one plumose distolateral seta, the outer plate nine terminal robust setae most denticulate, and the inner plate two plumose setae; right first maxilla, palp article 2 with five thick apicomedial robust setae, one apicolateral plumose seta, and two sub terminal apicolateral facial setae, the inner plate with two plumose apical setae; second maxilla outer plate apical margin with one small spinule, inner plate apicomedial corner with two weakly submarginal plumose setae and one slender naked seta. *Maxilliped* (Fig. 29): palp article 3 without ranks of thin setae on the inner ventral face, with four elongate apicolateral setae, the apex strongly produced and rugose, the dactylar face and mediofacial area of article 3 also rugose; inner plate with three thick tooth like robust setae, six plumose setae, and a single naked facial sub terminal seta apically, a medial row of three plumose setae, lacking medial ventrofacial robust setae, the peduncle bearing four slender medial setae basal to the inner plate, and one lateral seta; outer plate with two facial and two ventrofacial setae at M0.4 and M0.6 respectively, a row of six submarginal medio distal blunt tooth like robust setae, one plumose one armed and one naked terminal setae, and one naked ventro distal seta. *First gnathopod* (Fig. 30): coxal plate with a sparse row of short apical setae; fourth article bearing a small barely rugose posterior hump; carpus short, strongly lobate, the lobe rounded, without apical setae, and rugose; propodus trapezoidal, slightly longer than wide, the posterior angle with three short medial robust setae and two long, strong lateral robust setae, rounded and thus bearing a small rugose lobe, palm transverse, slightly convex, the dactylus with accessory spinules on the inner margin, and reaching to the palmar corner robust setae. *Second gnathopod* (Fig. 30): slightly larger than the first; the carpal lobe broader; the palmar corner more lobate, with two short medial robust setae and three lateral robust setae, dactylus bearing inner margin accessory spinules, and reaching to the palmar corner robust setae; coxa sparsely setulose apically, bearing a sac like gill. *Peraeopods* (Fig. 31): coxa 3 with a sparse row of short apical setae, coxa 4 moderately emarginate with three anteroventral setae and five posterior setae, peraeopods 3 and 4 subequal in length, longer than the second gnathopod, articles 4 and 5 spinous posteriorly, article 6 of the third leg bearing 2-2-2-2-2 posterior robust setae, and of the fourth leg 1-2-2-2-2-2 posterior robust setae; peraeopods 5, 6 and 7 similar, the coxae each bearing a weak posterior robust seta, the second articles expanded posteriorly, that of the sixth leg slightly narrower than the other two, ovate, postventrally moderately lobate, with short marginal setae, the posterior margins of the propodi without long setae except at the base of the dactyls, the dactyls a single facial and medial setule and without additional setules. *Gills* (Fig. 32): coxae 2–6 each bearing a single, sac like gill; sternites 2–6 each bearing a single simple, non dendritic gill. *Epimera* (Fig. 32): 1–3 without post-ventral teeth, although the third slightly acuminate; the first epimeron with no ventral robust setae, the second with two—one on the mid-anterior margin and one posterior-, the third with two anteroventral and one mid-ventral slightly facial robust setae, the posterior margins sinuous and with few setae. *Pleon* (Fig. 32): pleonites 1–3, bearing 2-2-3 post-dorsal marginal setae as well as fine marginal teeth; urosomite one without dorsal armaments; urosomites 5 and 6 each bearing a single dorso lateral seta posteriorly. *Pleopods* (Fig. 32): each with two retinacula and no accessory retinacula; peduncles naked except for three small basofacial setules on the first, and two small setae distolateral on the third; first

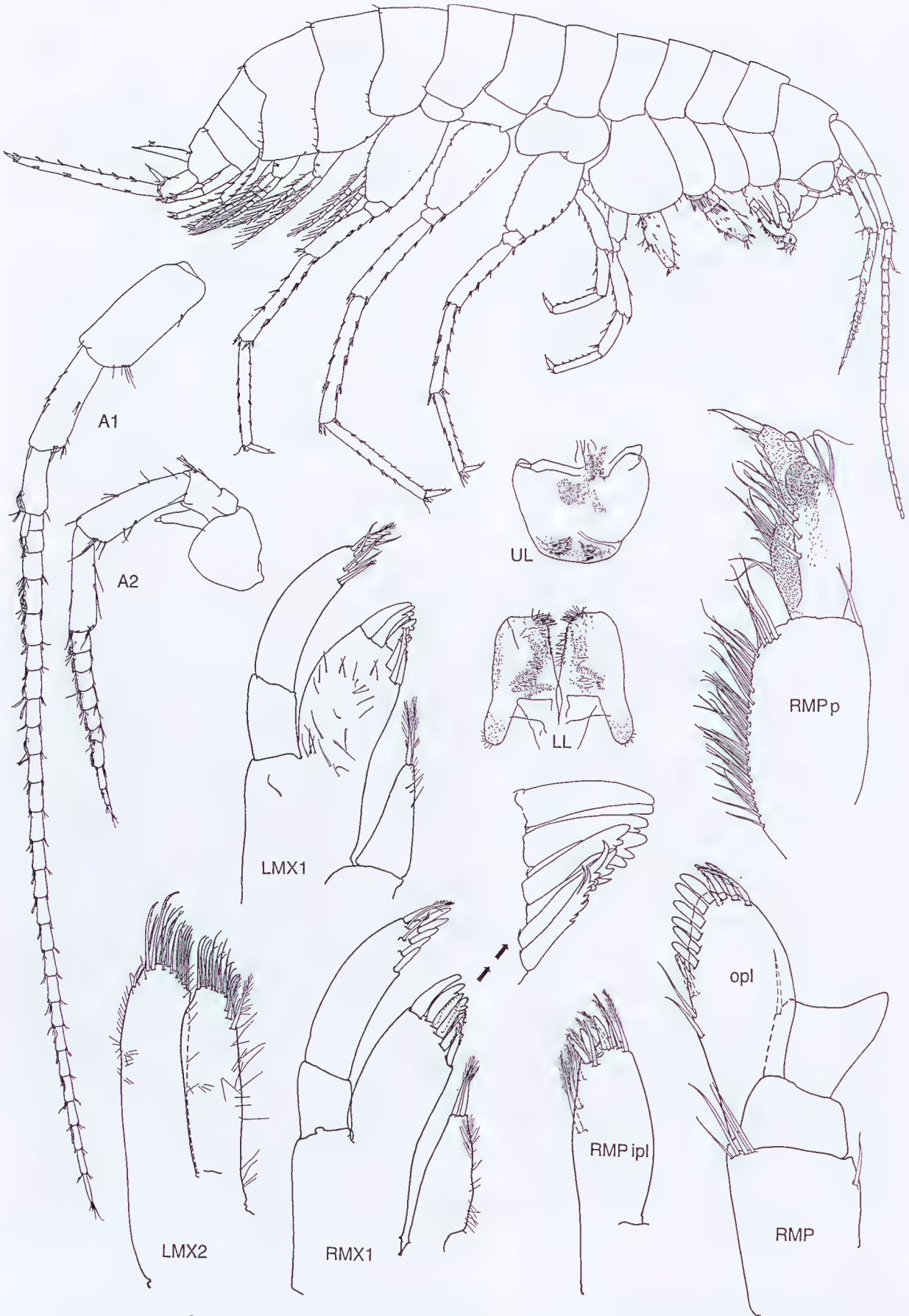

Fig. 29. *Wombeyanus botulosus* n.sp. holotype male "x" 7.5 mm; whole, antennae, mouthparts.

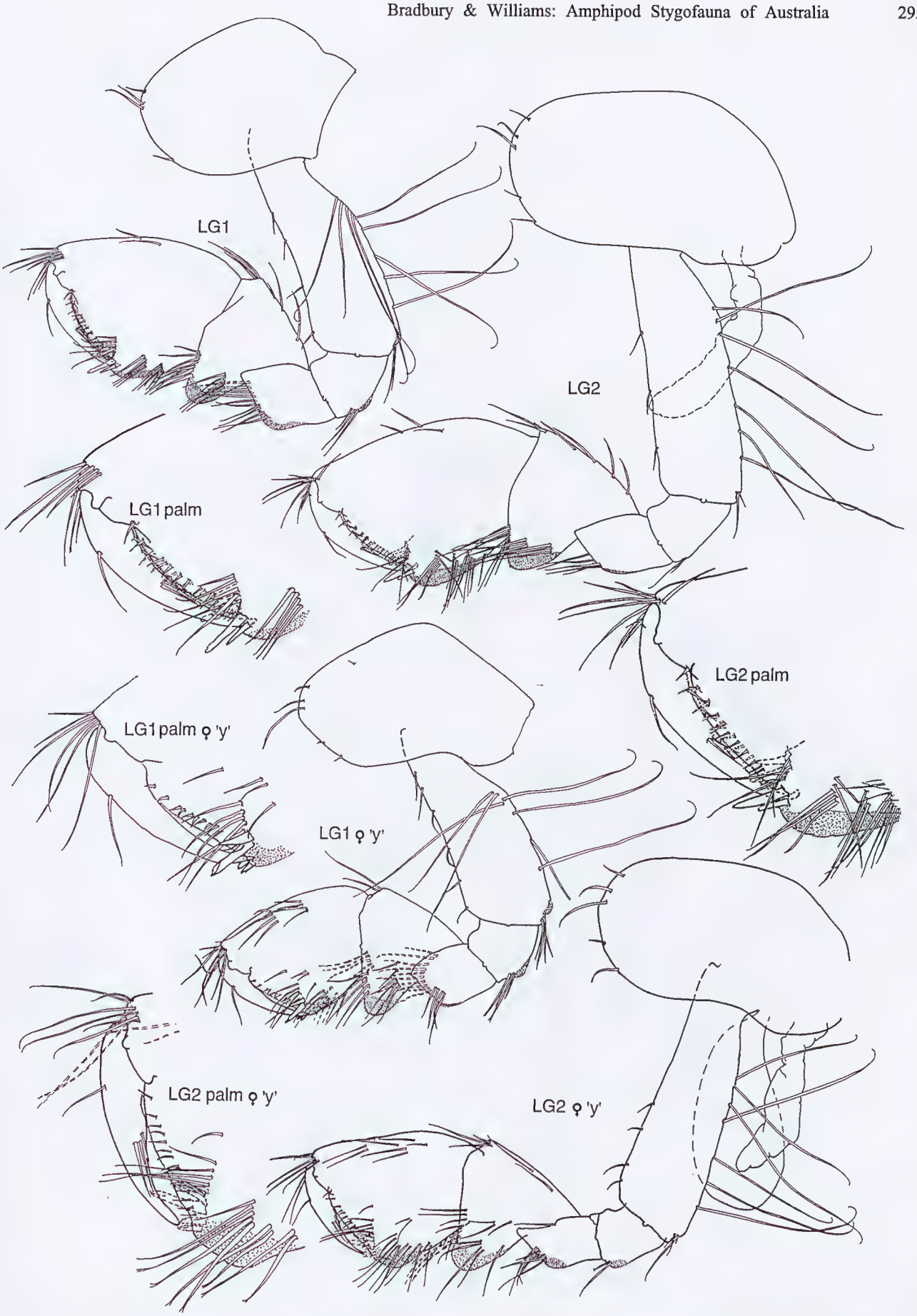

Fig. 30. *Wombeyanus botulosus* n.sp. holotype male "x" 7.5 mm; gnathopods (all drawings except those indicated). Allotype female "y" 7.5 mm gnathopods.

Fig. 31. *Wombeyanus botulosus* n.sp. holotype male "x" 7.5 mm; mandibles, peraeopods.

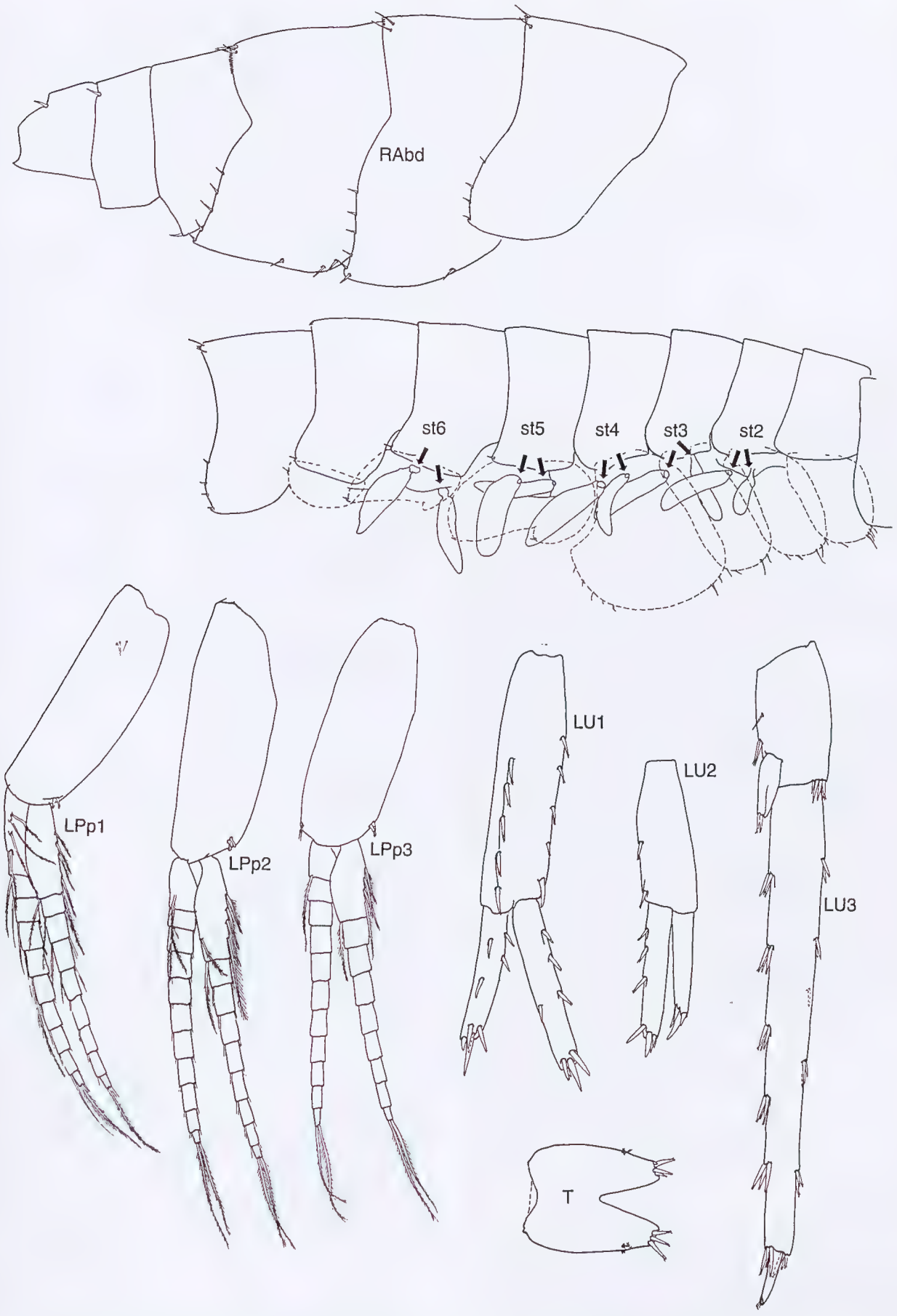

Fig. 32. *Wombeyanus botulosus* n.sp. holotype male "x" 7.5 mm; abdomen, gills, pleopods, uropods, telson.

article of the inner rami of each bearing terminally bifid basomedial setae and an additional ordinary plumose seta, rami of 9-9, 11-9, 11-9 lateral and medial articles respectively. *Uropods* (Fig. 32): third uropod extending well beyond uropods 1 and 2 in the whole animal; uropod lengths relative to uropod 1; uropod 2 0.65×, uropod 3 1.5×; first uropod peduncle length 1.4× medial and 1.8× lateral rami, the lateral margin without an apicodistal robust seta, with a row of five dorsal robust setae, the medial margin bearing five robust setae, rami of unequal length, both with two rows of short marginal robust setae, and four apical robust setae; second uropod peduncle approximately the same length as the medial ramus, with two short dorsolateral robust setae including the apical robust seta, outer ramus slightly shorter than the inner, only the medial ramus with three mediolateral robust setae, both rami with four terminal robust setae; third uropod peduncle as long as urosomite three, 0.5× the length of the outer ramus, bearing one facial and two distomedial robust setae and a distolateral row of five robust setae, the outer ramus of two articles, proximal article with transverse rows of robust setae arranged laterally 2-2-1-3-3 and medially 3-3-3-3-3, without setae, and lateral and medial groups of three terminal robust setae, the distal article short, approximately 0.12× proximal, three fine apical setules, the inner ramus short, 0.27× outer, with two simple apical setae only. *Telson* (Fig. 32): moderate length, approximately equal to the length of the peduncle of the third uropod, length 1.25× width; cleft 46%; apices with three short robust setae in a row, no other robust setae, and a pair of penicillate setules dorsolaterally at M0.75.

Description of allotype (female "y"). *Body*: length 7.5 mm. *First antenna*: peduncle ratio of lengths 10:9:6; primary flagellum of 23 articles, aesthetascs present on articles 4–20. *Second antenna*: peduncle articles 3–5 sparsely setulate, lengths of articles 4 and 5 equal; flagellum of eight articles. *Left mandible*: incisor with four teeth; lacinia mobilis four teeth, and a group of basofacial setae; accessory blades of thee chisel robust setae and three plumose setae; two bent brushy setae onto the base of the molar; molar triturative with a moderate posterior pappose seta; palp of three articles, ratio of lengths 8:20:21, article 2 with two medial setae, article 3 with setae 2B3C14D3E. *Right mandible*: incisor with four teeth; lacinia mobilis bifid and facially setose; accessory blades of two rakers and two plumose setae; three bent brushy setae onto the base of the molar; molar triturative, with a long posterior pappose seta; palp ratio of lengths of articles 8:22:23, second article with two medial setae, third article with setae 2B3C14D3E. *Left first maxilla*: palp with three slender apical robust setae, one with setules, two mediodistal and one apicofacial robust setae and two distofacial setae; outer plate with nine denticulate robust setae; inner plate with two apical plumose setae. *Right first maxilla*: palp with one stout setulate apical robust seta, an oblique distal row of five stout articulated robust setae, and a single apico facial slender seta. *First gnathopod* (Fig. 30): coxa with few apical setae; articles 2–4 with small posterior rugose lobes; carpus short with strong posterior rugose lobe; propodus trapezoidal, longer than wide, with small rugose posterior lobe, the rugosities extending to the corner robust setae; palmar corner with two small medial and two lateral robust setae, palm slightly oblique, straight, with few simple robust setae; dactyl with three accessory spinules on the inner margin and stiff spinules at the inner nail articulation. *Second gnathopod* (Fig. 30): coxa with few apical setae, bearing sac like gill and simple oostegite; articles 3 and 4 with small posterior rugose lobes; carpus with strong posterior rugose lobe; propodus with moderate posterior rugose lobe, palmar corner with two medial and three lateral robust setae, palm slightly convex and oblique, with moderate numbers of simple robust setae, dactylus with three accessory spinules on the inner margin and two stiff spinules at the inner nail articulation, and reaching the palmar corner robust setae. *Peraeopods*: peraeopod 3 similar to male, with few apical coxal setae, coxa bearing a broad oostegite; peraeopod 4 about the same length as three, coxa deeply emarginate, bearing a broad oostegite. *Pleopods*: peduncle of first ploepod naked, lateral ramus with 11 articles, inner with eight; second pleopod rami with ten and nine articles respectively; peduncle of third pleopod with two mid medial and two distolateral setae, rami of ten and eight articles respectively. *Uropods*: first uropod peduncle with three dorsomedial setae including the apical seta and four dorsolateral and one apicolateral setae, the outer ramus with two basomedial and two lateral robust setae, the inner with three medial and one lateral robust setae, each with four apical robust setae; second uropod peduncle with two dorsolateral and one apicolateral robust setae, and one dorsomedial and one apicomedial robust setae, each with four apical robust setae; third uropod parviramous, peduncle with three latero- and two mediodistal robust setae and four setae basal to the inner ramus; inner ramus short with only a single apical robust seta; outer ramus proximal article with transverse lateral robust seta groups 2-2-2-2-3 and three distolateral robust setae, the medial margin with 2-3-2-2-2-2 and five distomedial robust setae, distal article with a pair of small apical spinules, ratio of lengths of articles; peduncle 20, outer ramus proximal article 62, distal 8, inner ramus 10. *Telson*: similar to male, both lobes with two rather than three apical robust setae; lateral penicillate setules at M0.6.

Distribution. Bullio Cave, cave 2W2, Wombeyan Cave system, New South Wales, 34°19'S 149°59'E.

Jasptorus n.gen.

Etymology. Named for the type locality and the lumpy sternal gills; *torus* (Latin) protuberance or bulge.

Type species. *Jasptorus solepti* n.sp.

Diagnosis. Eyes absent; the first antenna long, peduncle article 1 subequal with article 2, calceoli present on peduncle and flagellum; second antenna peduncle longer than flagellum, calceoli present on flagellum. Second article of mandibular palp relatively short and poorly setose, setae of the third article BCDE. Inner plate of the first maxilla with two apical plumose setae, outer plate with nine robust setae, distal robust setae of the right palp articulated not fused. Coxae 1–4 sparsely setose ventrally; robust setae at the corner of the palm of both gnathopods 4 or more, palmar robust setae not crowded or bifid; dactyls of peraeopods without additional facial setules; coxal gill 7 absent, sternal gills on segments 2–6, and lumpy, not fully dendritic. Epimera without postventral teeth or facial robust setae or setae near the ventral margin. First uropod without an elongate robust seta at the apicomedial corner; both rami of first and second uropods with one robust seta row each, the third uropod strongly extended and without plumose setae. Telson of moderate length, cleft about 56%, the lobes moderately tumid, with only apical spination.

Additional description. Accessory blades (rakers) on mandibles with interraker plumose setae; additional penicillate setae

beyond rakers and riding onto base of molar, with ragged bent molarial setae and pappose seta. Lower lip uniform, inner lobes absent. Both plates of maxilla two with long apical setae; inner plate of maxilla one and outer plate of maxilla two covered with pubescence. Maxillipedal inner plate with a distal row of few plumose setae and two blunt naked robust setae, a medial basofacial to mid-facial row of five plumose setae and a pair of blunt naked tooth like robust setae; palp articles 2 and 3 naked laterally, well setose medially, article 3 with two pairs of non-comb robust setae near the base of the dactyl, the apex produced and rugose, the dactyl rugose. Dactyls of gnathopods without recumbent inner tooth like robust seta, with stiff spinules at the inner nail articulation, with additional spinules along the inner dactylar margin. Pleopods similar; peduncles bearing few setae, rami extending equally. Ventrodistal robust seta on urosomite one at the base of uropod 1 moderate to long.

Relationship. This genus bears lumpy sternal gills, a characteristic of *Wesniphargus* and is closest to that genus among the family. However, *Jasptorus* differs from *Wesniphargus* in: absence of eyes; shorter first peduncular article of the first antenna; sparse rather than moderate setation of the second article of the mandibular palp; asymmetry of the palp of the first maxillae; coxa 1 tapers apically, and the third coxa ovate rather than sub rectangular; propodi of gnathopods expanded apically, bearing posterior rugosities; palmar robust setae lacking triggers; second articles of peraeopods 5–7 moderately or weakly expanded posteriorly; third uropod distinctly parviramous, the outer ramus strongly extended and without medial plumose setae; telson cleft 56% rather than 85% and basally tumid. *Jasptorus* differs from *Tasniphargus* in the absence of eyes and of long dense setae and elongate basal flagellar articles on the first antenna, the presence of calceoli (on both antennae), presence of B and absence of A setae on the third article of the mandibular palp, nine rather than seven robust setae on the outer plate of the first maxilla; absence of triggers on palmar robust setae; coxal gill 6 not significantly reduced, sternal gills not dendritic; epimera without post-ventral teeth; clear asymmetry of rami of uropods 1 and 2; telson slightly tumid laterally. *Jasptorus* differs from *Neoniphargus* in the absence of eyes; sternal gills not dendritic; inner plate of first maxilla not ovate; dactyl of maxillipedal palp rugose as well as apex; palmar robust setae without triggers; corner robust setae of palms four or more rather than six or more; peraeopods elongate and slender; distodorsal robust setae of peduncles of uropods 1 and 2 sub apical; rami of uropods asymmetric, with few marginal robust setae; lobes of telson tumid basally. *Jasptorus* differs from *Yulia* in the absence of eyes; lack of long dense antennal setae; first antenna flagellar articles equal, not fused; C setae present on mandibular palp; inner plate of first maxilla with two rather than four apical setae; coxae poorly setose ventrally; robust setae of palmar corners four rather than eight; palmar robust setae not dense, bifid or with triggers; coxa 7 without gill; sternal gills lumpy rather than dendritic; peduncles of pleopods with no or very few setae; rami of uropods 1 and 2 unequal; third uropod strongly extended; telson moderately tumid.

Jasptorus solepti n.sp.

Figs 33–35

Etymology. Named for the slender form of the body: *soma* body, *leptos* thin.

Type locality. Cave WJ-10, Wee Jasper, New South Wales, 35°07'S 148°41'E.

Material examined. HOLOTYPE (Australian Museum P51372) male "a" 6.5 mm, other specimen in type series; male "b" 5 mm.

Diagnosis. As in the genus.

Description of holotype (male "a"). *Body* (Fig. 33): pleon with few dorsal arms, pleonites 1–4 with few setae, 5 and 6 with one dorsolateral robust seta each, length 6.5 mm. *Head*: rostrum small, eyes absent, lateral cephalic lobes prominent, antennal sinus moderate. *First antenna* (Fig. 33): length 0.8× body, 2.2× the second antenna, the peduncle shorter than the flagellum—64:151—with sparse setae; ratio of lengths of peduncular articles 10:9:6; flagellum of 25 uniform (excepting article 3 which is short), sparsely setulate articles; calceoli present on peduncle article 3 and flagellum articles 1, 2, 6, 8, 10, aesthetascs present on most flagellar articles; accessory flagellum 2-articulate reaching slightly beyond the end of article 1 of the primary flagellum. *Second antenna* (Fig. 33): length 0.36× body; peduncle 1.2× the flagellum, articles 4 and 5 subequal—22:23—and articles 3–5 with moderate ventral setation; flagellum of eight articles, weakly setose ventrally, calceoli present on articles 1–5. *Left mandible* (Fig. 33): palp relative lengths of articles 8:17:21; article 3 longer than 2, weakly falcate, with 1B3C21D5E setae, the second article bearing three inner marginal setae; incisor with four teeth and fine facial setae; lacinia mobilis with two weak teeth and an area of fine basofacial setae; accessory blades of three chisel robust setae and four plumose interraker setae; molar triturative with a long posterior pappose seta. *Right mandible* (Fig. 33): palp relative lengths of articles 8:23:27; third article longer than the second with 1B5C20D4E setae; incisor with four teeth; lacinia mobilis bifid, the anterior arm denticulate, the posterior with three teeth and an area of fine facial setules; two accessory blades (rakers), two plumose inter rakers, and three plumose and three hooked brushy setae onto the base of the molar; molar triturative without a posterior pappose seta. *Maxillae* (Fig. 33). Left first maxilla: palp article 2 with four submarginal mediodistal slender robust setae—three terminally armed and one naked—two armed and one naked distofacial robust setae and one distolateral plumose seta; outer plate with nine denticulate terminal robust setae and two short, slender, naked setae at the medio distal corner; inner plate with two apical plumose setae and one small naked medio distal seta. Right first maxilla: palp article 2 with five thick mediodistal to apical robust setae articulated to the segment, one apicolateral thin robust seta and one apicolateral rastellate seta; inner plate with two plumose apical setae. Second maxilla: outer plate with a small distolateral spinule; inner plate with two mediodistal (almost medial) plumose setae. *Maxilliped* (Fig. 33): palp article 3 with a row of thin setae on the inner margin, outer apex with three slender setae, apex face with two pairs of slender setae, dactyl with two medial and two sub terminal robust setae adjacent the nail, the apex strongly produced and rugose, as is the dactylar face; inner plate with two thick tooth like apical robust setae,

Fig. 33. *Jasptorus solepti* n.sp. holotype male "a" 6.5 mm; whole, antennae, mouthparts.

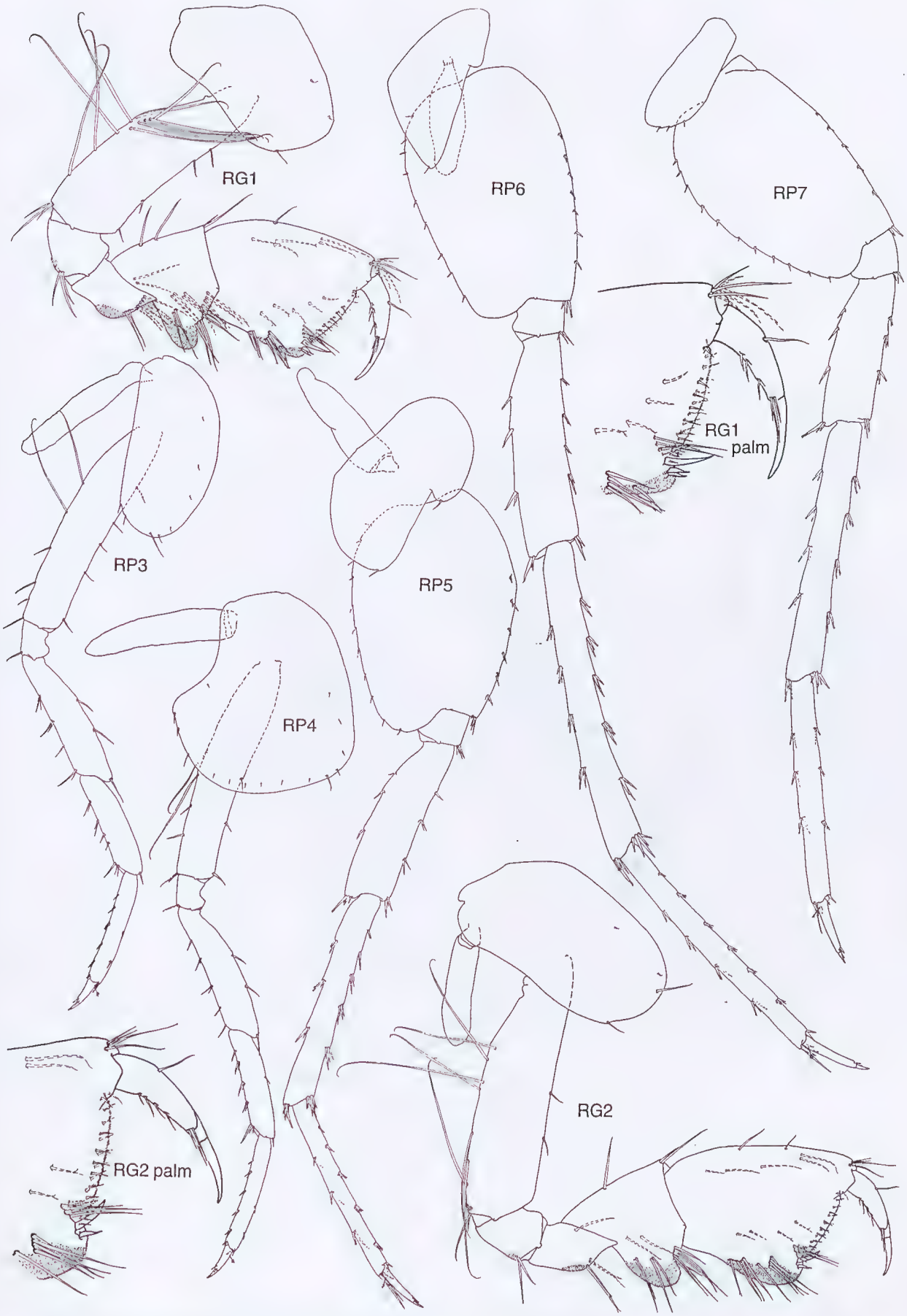

Fig. 34. *Jasptorus solepti* n.sp. holotype male "a" 6.5 mm; legs.

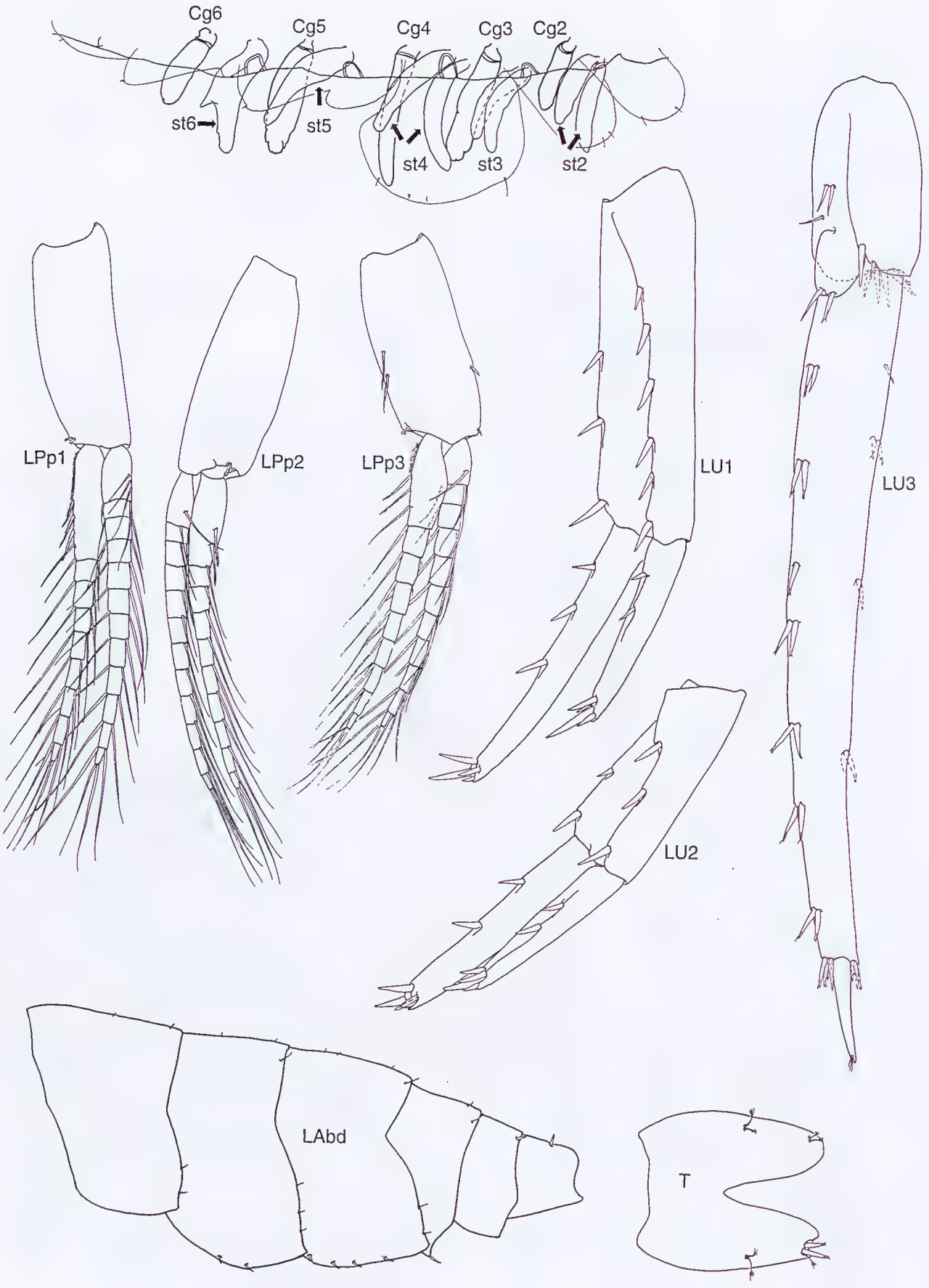

Fig. 35. *Jasptorus solepti* n.sp. holotype male "a" 6.5 mm; abdomen, gills, pleopods, uropods, telson.

several plumose and simple setae, and a row of medial submarginal plumose setae; outer plate with five basomedial slender setae, a row of naked tooth like robust setae medial sub marginal to mid distofacial, two distal plumose setae and a lateral sub marginal row of fine simple setae; peduncle bearing a pair of ventrofacial long setae basal to the inner plate. *First gnathopod* (Fig. 34): coxal plate with a single post-ventral seta only; article 3 with a small posterior rugose hump; article 4 with a moderate rugose hump; carpus short, strongly lobate and rugose, the lobe rounded and without setae; propodus trapezoidal, slightly longer than wide, posterior angle rounded, anteriorly prominent and rugose, the palmar corner marked by one medial and a long and two short lateral robust setae without bifurcations or triggers, the palm slightly oblique and convex, dactylus reaching to the corner robust setae, robust setae along the palm simple, not crowded. *Second gnathopod* (Fig. 34): slightly larger than the first, coxa bearing two apical setae, and a sac like gill; rugose carpal lobe larger than the first; rugose lobes of articles 2–4 smaller; posterior rugose lobe of the propodus more expanded than on the first gnathopod, the palmar corner marked by long and short lateral and medial robust setae, dactylus not reaching the palmar corner; the palm lined with simple setae. *Peraeopods* (Fig. 34): coxa 3 with few short and long apical setae; coxa 4 deeply emarginate with three anteroventral setae, one ventrofacial posterior seta, and several facial setules; peraeopods 3 and 4 subequal, longer than the second gnathopod, articles 4 and 5 posteriorly spinose, articles 6 with 2-2-2-2-2 and 1-2-2-2-2 robust setae respectively; peraeopods 5–7 similar, coxae with 1-1-3 robust setae on the ventral margins of the posterior lobes, the second article of each moderately expanded posteriorly (P5>P6>P7), with short sparse marginal setae and a moderate postero ventral lobe, posterior margins of propodi lacking long setae except for basodactylar setae, dactyls without accessory setules apart from the usual one medial and facial setules. *Gills* (Fig. 35): coxae 2–6 bearing simple sac like gills, coxa 7 without gill; sternites 2–6 each with a pair of lumpy, incipiently dendritic gills attached to the anterior lateral edge of each segment. *Epimera* (Fig. 35): without postventral teeth, although each slightly acuminate; posterior margins moderately convex, with 2-3-2 setae; with 0-2-4 ventrofacial robust setae. *Urosomite one* (Fig. 35): with a short robust seta at the base of uropod 1. *Pleon* (Fig. 35): pleonites 1–4 with few dorsal armaments; pleonite 5 with a single posterolateral robust seta, pleonite 6 with one mid dorsal robust seta. *Pleopods* (Fig. 35): similar, each with two retinaculae and no accessory retinaculae; peduncle of pleopod 3 only with two medial and two facial setae; rami with 12-9, 12-10, 11-9 lateral and medial articles. *Uropods* (Fig. 35): third uropod extending well beyond uropods 1 and 2 in the intact specimen; lengths relative to uropod 1—uropod 2 0.64×, uropod 3 1.54×; first uropod peduncle approximately equal to the third urosomite, length 1.9× lateral ramus, 1.2× medial ramus, the outer margin with a single subapical robust seta and a row of five short robust setae, the inner margin with a row of two short robust setae and a single distal robust seta; rami of unequal lengths, medial 1.3× lateral, both with a single row of dorsal robust setae—the lateral ramus with two lateral setae, the medial ramus with three medial setae-and each with four apical robust setae; second uropod peduncle 0.9× inner ramus, 1.2× outer ramus, with three short dorsolateral and two short dorsomedial robust setae, the outer ramus shorter than the inner—27:36—both with only one row of short robust setae—lateral ramus with two lateral robust setae and medial ramus with two medial robust setae, each with four apical robust setae; peduncle of the third uropod 0.26× length of outer ramus, as long as urosomite three, with three mediofacial setae, two mediodistal robust setae basal to the inner ramus, and a distal transverse lateral row of five robust setae; proximal article of the outer ramus with four transverse lateral robust seta rows of 1-2-1-1 robust setae, seven transverse medial rows of 2-2-1-2-2-2-2 robust setae and terminal lateral and medial rows of three and four robust setae basal to the distal article; distal article with three small terminal setules; inner ramus length 0.09× outer, with two apical setae only. *Telson* (Fig. 35): moderate length, equal to urosomite three, the length 1.1× width; cleft 56%; apices with two short setae set in a notch on the left side, no robust setae or notch on the right, but a pair of sub terminal penicillate setules; lobes moderately tumid, with paired dorsolateral penicillate setules at M0.6 on either lobe.

Description of male "b". *Body*: length 5 mm. Similar to male "a", except in the following. *First antenna*: left peduncle third article with mediodistal calceolus; accessory flagellum of two articles, extending to M0.8 of the second article of the primary flagellum; primary flagellum of 21 articles, with aesthetascs on articles 5–21; right primary flagellum of nineteen articles. *Second antenna*: left flagellum of seven articles with calceoli present on articles 1–4; right flagellum of seven articles, with calceoli on articles 3–5. *Mandibles*: both mandibular palp articles 3 with setae 1B3C11D3E. *Pleopods*: left first pleopod rami with four medial and five lateral articles; right first pleopod with seven and eight articles respectively; second pleopod with 7-8 and 9-7 articles respectively; third pleopod with 6-8 and 6-8 articles respectively. *Uropods*: peduncle of first uropod with three dorsolateral and one apicolateral and two dorsomedial and one apicomedial robust setae; outer ramus with one medial and one lateral robust setae; inner ramus with two medial and one lateral robust setae, both rami with four apical robust setae; peduncle of second uropod bearing one dorsolateral and one apicodorsal, tow dorsomedial and one apicomedial robust setae; outer ramus with one each medial and lateral robust setae, inner ramus with two each medial and lateral robust setae. *Epimera*: second epimeron with one rather than two facial robust setae near the ventral margin.

Distribution. Cave WJ10, Wee Jasper, New South Wales, 35°07'S 148°41'E.

Neoniphargus Stebbing, 1899

Neoniphargus Stebbing, 1899: 424.
Unimelita Sayce, 1901: 237–238.

Type species. *Neoniphargus thomsoni* Stebbing, 1899 (= *Niphargus montanus* Thomson, 1893, a homonym).

Relationship. For generic diagnosis, additional description, keys and discussion of relationships see Williams & Barnard (1988: 123–125).

Composition. This genus contains seven species. We here describe a further three species.

Neoniphargus coolemanensis n.sp.

Figs 36–38

Etymology. Named for the type locality.

Type locality. First water trap, Murray Cave (cave CP3), Cooleman Plain, Kosciusko National Park, New South Wales, 35°22'S 149°03'E.

Material examined. HOLOTYPE (Australian Museum P51373) female, 6 mm; collected by S. Eberhard; 20 January, 1994.

Diagnosis (female only): first peduncular article of the first antenna longer than the second; second antenna without calceoli; second article of the mandibular palp longer than the third, and moderately sotose, setae of the third article BCDE; palmar corners of gnathopods without special medial robust setae; fourth coxa deeply emarginate, dactyls of peraeopods 3–7 multispinous medially, articles 4–6 of peraeopods 3–7 moderately setose, with elongate basodactylar setae on legs 5–7, anterior margins of sixth article with 1-4-4 transverse robust seta sets (as well as locking robust setae); coxae 5–7 with 1-1-3 weak robust setae on the posterior lobe. Coxae 2–7 bearing gills, the seventh reduced; lumpy to barely dendritic gills present on sternites 2–6. Epimera without facial armaments, or postventral teeth; third uropod extends slightly beyond uropods 1 and 2 in the whole animal; robust setae of uropods 1 and 2 all short; peduncle of uropod 3 0.6× the length of the outer ramus; robust setae of outer ramus arranged in sets of 2-3-3 lateral, 1-2 medial, with no plumose setae; inner ramus bearing one apical robust seta, and no facial setae. Telson cleft about 60%, each lobe bearing three apical robust setae and a dorsal pair of robust setae.

Description of holotype (female). *Body* (Fig. 36): pleon with few setal dorsal armaments, the urosomite three bearing two pairs of dorsal robust setae, pleonites with few dorsal setae, length 6 mm. *Head*: small, eyes small. *First antenna* (Fig. 36): length 0.5× body, 1.4× the second antenna, peduncle less than the length of the flagellum, ratio of lengths of articles 50:33:23, setae sparse, calceoli and aesthetascs absent; accessory flagellum 2-articulate, extending to M0.2 of the second article of the primary flagellum; primary flagellum of nineteen uniform articles with very sparse setation. *Second antenna*: length 0.3× body, peduncle longer than the flagellum—1.5×, articles 4 and 5 subequal, articles 3–5 with moderate ventral setation, flagellum with nine articles, weakly setose ventrally, calceoli absent. *Left mandible* (Fig. 36): palp of three articles, ratio of lengths of articles 10:32:24, article 2 with ten inner marginal setae, article 3 weakly falcate, with 1B3C11D5E setae; incisor with five teeth; lacinia mobilis with three teeth; accessory blades of three chisel robust setae, three plumose robust setae; molar triturative, bearing a single brushy anterior seta and short posterior pappose seta. *Right mandible* (Fig. 36): palp article 2 with 12 medial setae, article 3 with 2B2C10D5E setae; incisor with five teeth; lacinia mobilis bifid and denticulate; two accessory blades and two inter-raker plumose setae; molar bearing long posterior pappose seta. *Maxillae* (Fig. 36). First maxillae: second article of the palp of the left first maxilla with six thin apical robust setae and two sub terminal facial setae; outer plate with nine robust setae, most denticulate; inner plate with two plumose apical setae; right first maxilla palp article 2 with four thick apicomedial robust setae articulated to the segment, one apicolateral thin robust seta and three thin ventro facial robust setae; outer plate with ten apical denticulate robust setae; inner plate with two plumose apical setae. Second maxilla: both plates with curved apical setae; inner plate with two medial sub apical plumose setae; outer plate with two subdistal naked lateral setae. *Maxilliped* (Fig. 36): palp articles 2 and 3 with ranks of setae on the inner margin and sub marginal face, and a few distolateral setae, apex of article 3 strongly produced and bearing rugosities, dactyl with four accessory spinules on the inner margin, and distofacially rugose; inner plate apex with three thick tooth like robust setae, two plumose setae and a naked seta, a submarginal medial row of five plumose setae, but no ventrofacial robust seta; outer plate with a medial oblique row of moderate to long naked robust setae distofacially, a row of six faciomedial to distomedial naked tooth like robust setae, apically a naked tooth like robust seta and armed tooth like robust seta, two raker setae and one plumose seta, and three slender disto lateral setae. *First gnathopod* (Fig. 37): coxal plate tapering apically, with an apical rows of moderate length setae; articles 2 and 3 each bearing a small rugose posterior lobe; articles 4–6 with strong rugose lobes; carpus shorter than propodus, posterior lobe well developed, rugose, rounded and not setose apically; propodus trapezoidal, slightly longer than wide, bearing paired posterior rugose lobes, corner of the palm with three short medial robust setae and two strong, armed lateral robust setae; palm transverse, slightly convex, with moderate numbers of non-bifid robust setae, dactylus reaching the palmar corner robust setae. *Second gnathopod* (Fig. 37): larger than the first; coxa sparsely setose apically bearing a sack like gill and a broad, naked oostegite; carpal lobe longer and more keel like than the first; propodus with a distinct pair of rugose lobes larger than in the first, palmar corner with three short medial and two long lateral robust setae, dactylus reaching the palmar corner robust setae, palm transverse, slightly convex, bearing moderate numbers of simple robust setae. *Peraeopods* (Fig. 37): coxa 3 with an apical sparse row of moderate length setae; coxa 4 deeply emarginate with three anteroventral setae and four posterior setae; peraeopods 3 and 4 longer than the second gnathopod, subequal in length, articles 4 and 5 spinose posteriorly, articles 6 with robust seta formula 1-1-2-2-3 and 1-1-3-2-3, respectively; peraeopods 5–7 similar, coxae bearing 1-1-3 weak robust setae on the posterior lobe, articles 2 expanded posteriorly (P5<P6<P7), and slightly to moderately lobate postventrally, with short and moderately slender posterior setae, propodus of leg five naked posteriorly, of 6 and 7 with sparse short and long setae, long setae present at the bases of the dactyls of peraeopods 6 and 7; dactyls three to seven each with several accessory setules (2-3-1-4-3) on the inner margin; coxae 2–5 each bearing an oostegite. *Gills* (Fig. 38): coxae 2–7 each with a simple sac

Fig. 36. *Neoniphargus coolemanensis* n.sp. holotype female 6 mm; whole, antenna, mouthparts.

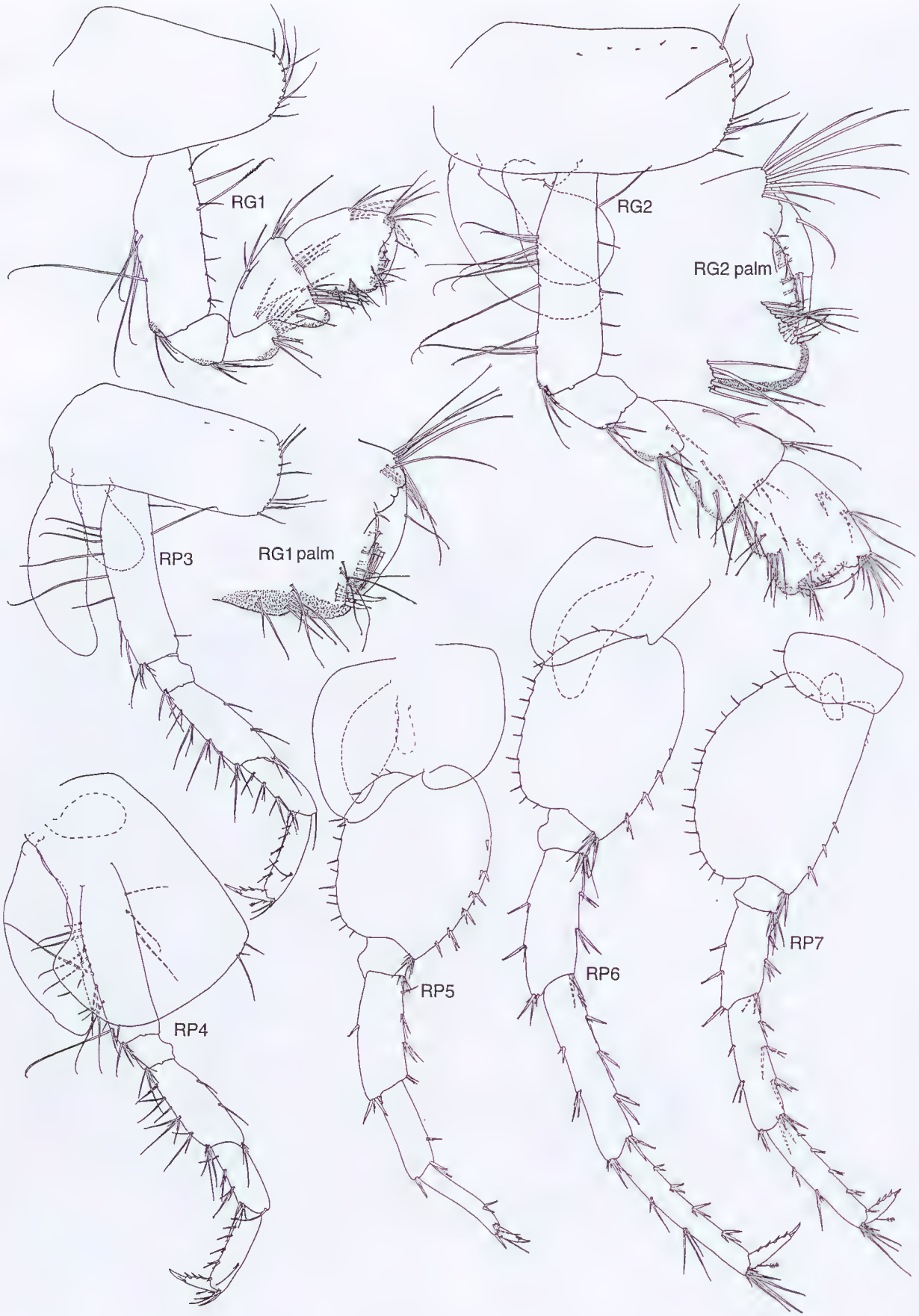

Fig. 37. *Neoniphargus coolemanensis* n.sp. holotype female 6 mm; legs.

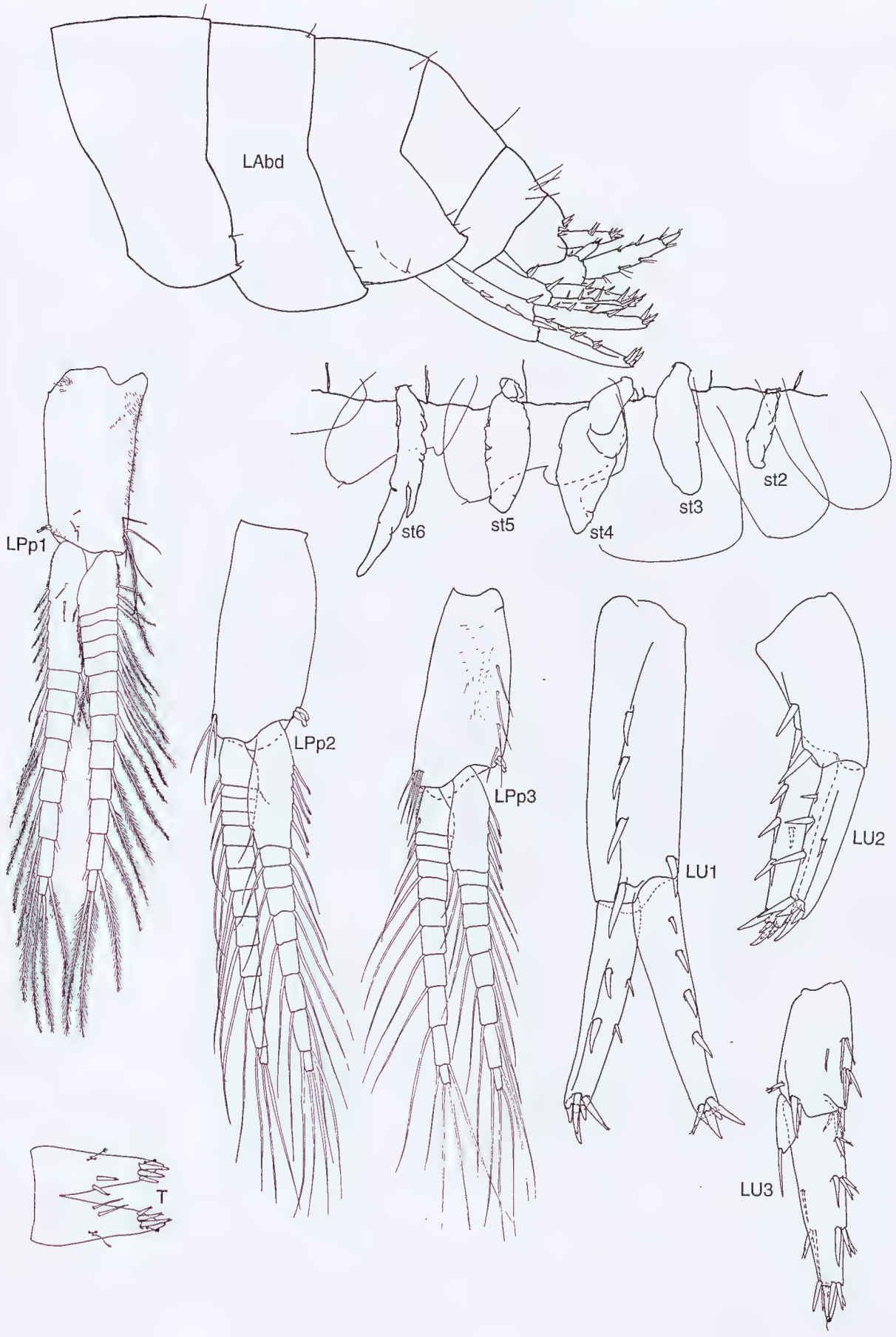

Fig. 38. *Neoniphargus coolemanensis* n.sp. holotype female 6 mm; abdomen, gills, pleopods, uropods, telson.

like gill, that of coxa 7 reduced; sternites 2–6 bearing budded or partially dendritic gills attached on the anterior lateral edge of each. *Epimera* (Fig. 38): without postventral teeth, the posterior margins slightly convex on E1, straight on E2 and concave on E3; all without ventral robust setae; posterior setae sparse—2-3-3. *Pleon* (Fig. 38): pleonites 1–5 with few dorsal setae or robust setae; pleonite 6 bearing a pair of dorsal and a pair of dorsolateral robust setae basal to the telson. *Pleopods* (Fig. 38): with two retinacula each, no accessory retinacula, the peduncles each with several setae; rami of nine medial articles each and 13-13-11 lateral articles respectively. *Uropods* (Fig. 38): third uropod extending slightly beyond the first and second in the whole animal, uropod lengths relative to the first—uropod 2 0.7×, uropod 3 0.6×. First uropod: peduncle length 1.2× the medial ramus, 1.5× lateral ramus, outer margin with one apicodistal robust seta and a row of short dorsal robust setae, medial margin with a single apicodistal robust seta; rami of unequal lengths, lateral ramus shorter and bearing two reduced rows of marginal robust setae the inner row short; and five apical robust setae; medial ramus with only a medial row of four robust setae, and four apical robust setae. Second uropod: peduncle approximately the same length as the rami, with three moderate length to long dorsolateral robust setae (including one apical robust seta); outer ramus slightly shorter than the inner, each with two rows of short marginal robust setae, apices with four and five robust setae respectively. Third uropod: parviramous, peduncle length approximately 0.5× outer ramus, as long as urosomite three, bearing two pairs of medial and two groups of dorsal robust setae, as well as a distal row of five robust setae basal to the outer article; outer ramus proximal article with three lateral transverse robust seta rows of 2-3-3 robust setae and an apical group of three robust setae, as well as two medial rows of 1–2 robust setae and a terminal group of three robust setae; distal article with a single small terminal setule; inner ramus short, 0.27× length of outer ramus, with a single moderately long terminal robust seta. *Telson* (Fig. 38): short, approximately the same length as urosomite three, length 1.4× width; cleft 77%; apices of each lobe with three sub distal robust setae and a single lateral penicillate setule, two dorsal robust setae medially at M0.4 to M0.5, and a submarginal lateral pair of penicillate setae at M0.4; lobes not tumid.

Relationship. This species differs from others of the genus in: ratio of lengths of peduncular articles of the first antenna 10:6.5:5.4, cf. 10:8:5 to 10:11:6, the second article being reduced; length of the first article of mandibular palp reduced, relative lengths being 8:39:30 cf. 8:25:23 to 8:20:24; robust setae at the palmar corner 5 or 6, rather than 6+; robust setae along the palm are not dense; dactyls of peraeopods are multi-spinous, but differ from *Neoniphargus spenceri*; robust setae of the inner rami of first and second uropods are reduced to one row; telson cleft 80% rather than 60%; lateral penicillate setules of the telson are at about M0.5 rather than M0.6; plumose setae are absent between rakers and base of the molar. This species keys to *N. spenceri* in Williams & Barnard (1988), but differs in: the small size of eyes; shorter first antenna; longer accessory flagellum; longer second antenna; mandibular palp second article more setose medially, third article with fewer BC setae and more E setae; second article of first maxilla with nine or ten robust setae, rather than seven; inner plate of maxilliped with three rather than two apical robust setae, but fewer plumose setae; first gnathopod coxa moderately setose apically, the fourth article with a moderate posterior rugose hump, articles 2 and 3 also with posterior rugosities and small hump, carpus moderately long, almost as long as propodus, propodus with fewer lateral corner robust setae, the palm slightly convex; peraeopods generally less spinous, dactyls bearing 2-3-1-4-3 accessory spinules; sternal gills are not fully dendritic; epimera without postventral teeth; uropod 3 not as strongly extended; telson longer than wide, cleft 77% rather than 56%, fewer dorsal robust setae, lateral penicillate setules more basal. This species differs from *N. secus* in: possessing eyes; the body more robust, and coxal plates longer; accessory flagellum is longer than the first article of the primary flagellum; flagellum of the second antenna is of nine rather than seven articles; the second article of the mandibular palp is more setose medially; coxae 1–3 are moderately setose distally; carpus of the second gnathopod relatively long; dactyls of peraeopods multispinous; coxa 7 bears a small gill; sternal gills are less dendritic; third uropod is only slightly extended beyond uropods 1 and 2; telson is more slender and more deeply cleft and bearing additional dorsal robust setae, the penicillate setules more basal. *Neoniphargus coolemanensis* differs from *N. richardi* in: possessing eyes; the body is less slender; coxal plates larger; flagellum of second antenna longer; second article of mandibular palp bearing more setae; mandibular palp more spinous, the inner plate less pubescent; carpus of second gnathopod relatively longer; dactyls of peraeopods multispinous; coxa 7 with a small gill; sternal gills less dendritic; third uropod shorter; telson slender and not tumid, with dorsal robust setae as well as more apical robust setae.

Distribution. Murray Cave (cave CP3), Cooleman Plain, Kosciusko National Park, New South Wales, 35°22'S 149°03'E.

Neoniphargus secus n.sp.

Figs 39–41

Etymology. From *secus* (Latin); otherwise or different.

Type locality. Gurangah Cave, cave 321, Wombeyan Cave system, New South Wales, 34°19'S 149°59'E.

Material examined. HOLOTYPE (Australian Museum P51374) female "a" 8 mm, PARATYPE (Australian Museum P51375) female "b" 5 mm, three other small females in the type series; collected by S. Eberhard; 17 March, 1993.

Diagnosis. Article 1 of the peduncle of first antenna slightly longer than article 2, calceoli absent from both antennae, mandibular palp article 2 longer than article 3 with very few setae (3R2L ventral, 1L1R dorsal), BCDE setae present on article 3. The fourth coxa moderately emarginate, dactyls of legs three to seven with only one medial and one facial spinules, legs 5–7 , articles 4–6 without slender setae except for a few short basodactylar setae, and articles 6 anterior margins with one, five and four robust seta sets respectively, coxae 5–7 with 3-1-2 weak robust setae on the posterior lobe.

Fig. 39. *Neoniphargus secus* n.sp. holotype female "a" 8 mm; whole, antennae, mouthparts.

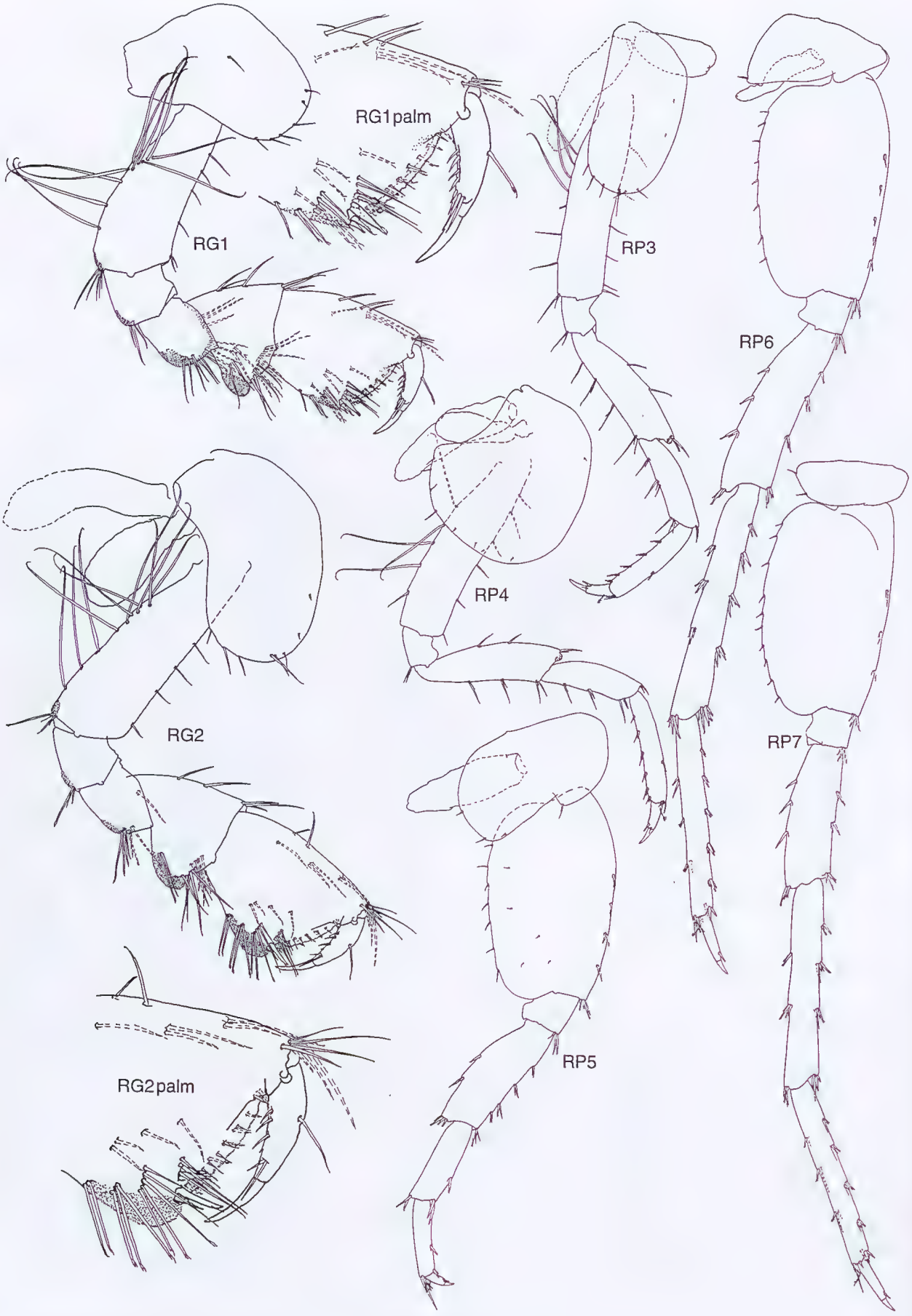

Fig. 40. *Neoniphargus secus* n.sp. holotype female "a" 8 mm; legs.

Gills present on coxae 2–6, and dendritic sternal gills present on sternites 2–6. Epimeron three only bearing ventrofacial robust setae. Uropod 3 extends well beyond uropods 1 and 2 in the intact specimen, all robust setae of uropods 1 and 2 short, the peduncle of uropod 3 0.3× the length of the outer ramus, which bears robust setae arranged in rows both laterally (1-2-2-3) and medially (2-3-2-2), without plumose setae; the inner ramus with a single apical robust seta, lacking other arms. The telson cleft 40%, each lobe bearing three sub apical robust setae only.

Description. *Body* (Fig. 39): pleon not armed dorsally, with few setae, pleonites 5 and 6 bearing no dorsal robust setae, length 8 mm. *Head*: rostrum small, eyes absent. *First antenna* (Fig. 39): length 0.5× body, 2.3× the second, flagellum of nineteen articles, peduncle shorter than the flagellum, ratio of lengths 10:8:6, setae sparse, calceoli absent, aesthetascs present on flagellum articles 2–18, flagellar segments uniform, sparsely setulate; accessory flagellum 2-articulate, equal to article 1 of the primary flagellum. *Second antenna* (Fig. 39): length 0.25× body, peduncle 1.7× the flagellum, articles 4 and 5 subequal, articles 3–5 moderately setate ventrally, flagellum 7-articulate, weakly setulose, without calceoli, but bearing small aesthetascs on flagellar articles 2–6. *Left mandible* (Fig. 39): palp article 3 shorter than article 2, weakly falcate, almost linear, bearing 2B3C9D4E setae, article 2 with two medial and one lateral setae; incisor with five teeth; lacinia mobilis with four teeth; accessory blades of three chisel robust setae with four interraker plumose setae plus five additional plumose setae beyond the rakers onto the base of the molar; molar bearing moderate posterior pappose seta without brushy basal setae. *Right mandible* (Fig. 39): palp with 2B4C12D5E setae; incisor with five teeth; lacinia mobilis bifid and denticulate; accessory blades of two chisel robust setae and two plumose robust setae plus six additional plumose setae onto the base of the molar; molar bearing a long posterior pappose seta. *Maxillae* (Fig. 39): article 2 of the palp of left first maxilla with four thin apicomedial robust setae, two subterminal facial setae and a stout setulate laterodistal robust seta; outer plate with nine mostly denticulate robust setae; inner plate with three apical plumose setae; palp article 3 of the right first maxilla with a mediodistal row of four stout robust setae, two armed slender facial robust setae and one distolateral stout setulate robust seta; the outer plate bearing nine denticulate robust setae, the inner plate two plumose apical setae; both plates of the second maxilla bearing long curved apical setae, outer plate with a single small disto lateral seta, inner plate with two medio distal plumose setae. *Maxilliped* (Fig. 39): palp article 3 with moderate numbers of setae on the inner face, a row of six setae at the base of the dactyl, the apex strongly produced, the lateral face of the article, apex and inner distal face of the dactyl all rugose, dactyl with three accessory spinules on the inner edge, the nail naked; inner plate apex with two facial and one ventral stout, naked tooth like robust setae, five facial and two ventral plumose setae and one naked seta, the inner margin with a row of seven plumose and one naked setae; outer plate with three mid-medial rows of 2-1-5 long setae, a distofacial row of five stout naked tooth like robust setae, one plumose and two rastellate laterodistal robust setae in a row and a small naked apical seta. *First gnathopod* (Fig. 40): coxal plate with a sparse apical row of short setae; articles 2, 3 and 4 with small posterior rugose lobes; carpus short, with a large rugose posterior lobe rounded and not setose apically; propodus trapezoidal, longer than wide, with a distinct rugose palmar corner bearing three lateral and one medial robust seta, the palm transverse to slightly oblique, moderately convex, palmar robust setae simple and not crowded; dactylus reaching the end of the palm, with several accessory spinules along the inner margin, and stiff spinules near the inner nail articulation. *Second gnathopod* (Fig. 40): larger than the first; coxa bearing few apical setae, a sac like gill and broad oostegite; articles 2–4 bearing small posterior rugose lobes; carpal lobe similar to the first gnathopod; palmar corner expanded by presence of a rugose lobe, corner robust setae being two short medial and four lateral, the dactyl reaching the inner edge of the lobe, bearing small recumbent inner tooth like robust seta at M0.6. *Peraeopods* (Fig. 40): coxa 3 with short sparse apical setae; coxa 4 moderately emarginate, with four anteroventral setae, without posterior setae; peraeopod 3 subequal with four, longer than the second gnathopod, articles 4 and 5 spinose posteriorly, articles 6 with 2-2-2-2 and 1-2-2-2-2 robust setae respectively; peraeopods 5–7 similar—five shortest, six longest; coxae 5–7 bearing 1-1-2 setae on the posterior lobe, the second article of each expanded posteriorly, slightly to moderately post-ventrally lobate with short posterior setules, posterior margins of the propodi lacking long setae except for long subdactylar setae; dactyls of legs three to seven with only a single facial spinule and small medial spinule. *Gills* (Fig. 41): simple sac like gills present on coxae 2–6; dendritic gills present on sternites 2–6, attached to the anterior lateral edge of each. *Epimera* (Fig. 41): 1–3 without postventral teeth, posterior margins slightly convex to straight, each with two small setae, posteroventral margin of the third epimeron with three small robust setae. *Pleon* (Fig. 41): pleonites 1–6 with sparse dorsal setation; pleonite 5 with a single distal dorsolateral robust seta. *Pleopods* (Fig. 41): peduncles each with two retinacula, pleopod 1 with a single accessory robust seta; peduncles without setation except pleopod 3 which bears three basomedial and two distolateral setae; rami with 10-7, 9-7 and 10-8 lateral and medial articles respectively. *Uropods* (Fig. 41): third uropod elongate, extending well beyond uropods 1 and 2 in the intact specimen, uropod lengths relative to uropod 1—uropod 2 0.64×, uropod 3 1.16×; first uropod peduncle length 1.5× outer ramus, outer margin with one apicodistal robust seta and a row of four short dorsal robust setae, the inner margin with three short robust setae and a moderate length apical robust seta; rami unequal in length (inner ramus 1.2× outer), the inner ramus with two weakly represented rows of short setae, the outer ramus a lateral row only, both rami with four apical robust setae; second uropod peduncle approximately the same length as the inner ramus, longer than the outer ramus, with two medial and three laterodorsal robust setae; rami each with two poorly represented rows of short marginal robust setae and four apical robust setae; peduncle of the third uropod as long as the third urosomite, 0.3× the length of the outer ramus, bearing four facial setae, two robust setae basal to the inner ramus and a transverse distolateral row of four robust setae; outer ramus proximal article with transverse lateral and transverse medial rows of 1-2-2-3 and 2-3-2-2 robust setae respectively, each side with distal clusters of three robust setae; distal article small, 0.1× proximal, with small apical setules; inner ramus small, 0.16× outer ramus, naked except for a single apical seta. *Urosomite one* (Fig. 41): at the base of uropod 1 bearing a small articulated robust seta. *Telson* (Fig. 41): short, 1.2× as long as broad; cleft 40%; subapices of each lobe bearing three short robust setae, the right lobe with a small additional seta distolaterally; a pair of dorsolateral penicillate setules at M0.6 on either lobe.

Female "b" 5.5 mm and two other small females. Essentially as for female "a", with minor differences only.

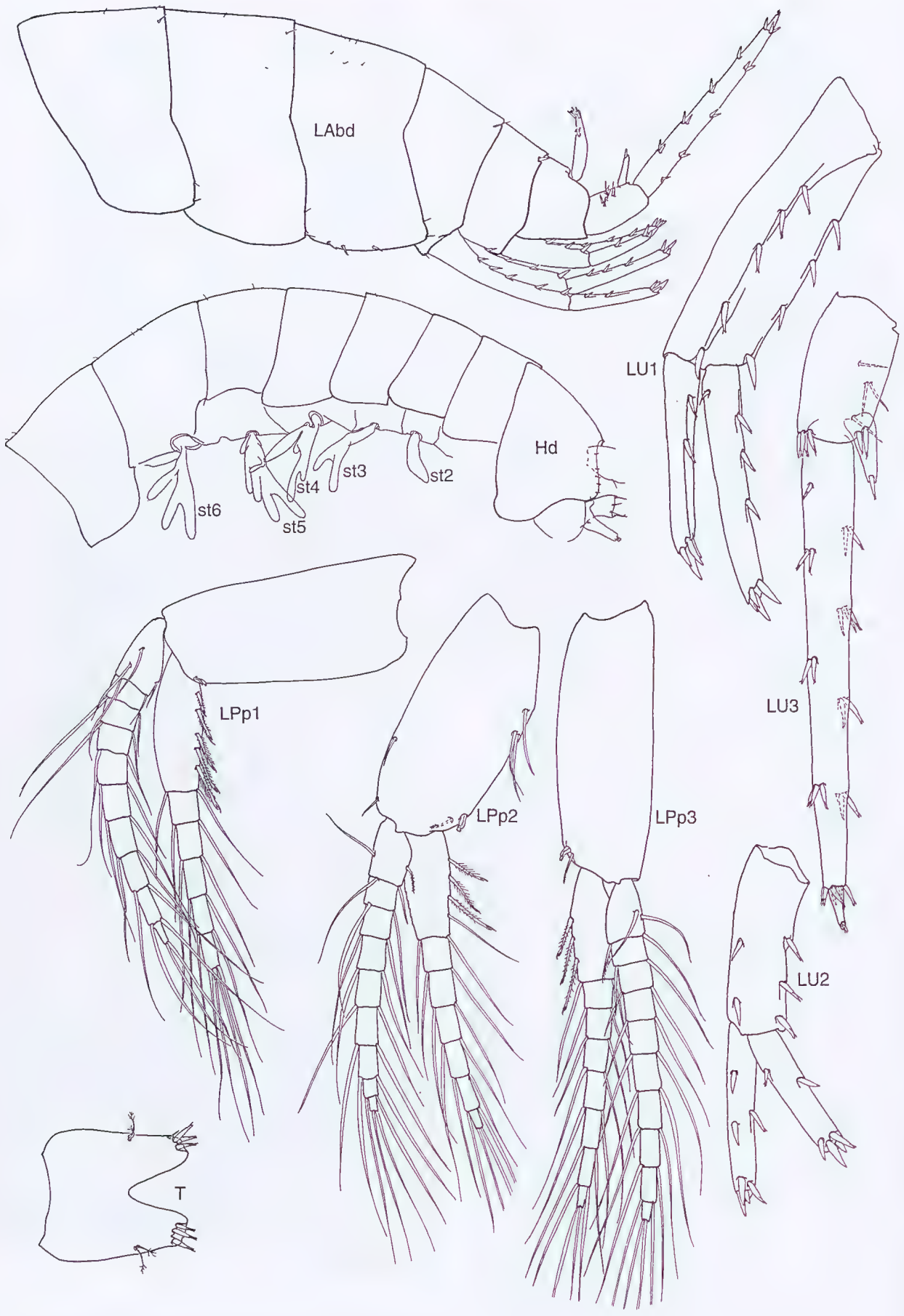

Fig. 41. *Neoniphargus secus* n.sp. holotype female "a" 8 mm; abdomen, gills, pleopods, uropods, telson.

Relationship. This species differs from others of the genus *Neoniphargus* in that eyes are totally absent; the first article of the mandibular palp is relatively longer; palmar corner robust setae are fewer and palmar robust setae less dense and without triggers; no accessory retinaculum is present but the third pleopod bears an accessory seta adjacent the retinacula; the telson is less cleft. *Neoniphargus secus* differs from *N. richardi* in: lower lip without posterior rugosities; mandibular palp with more E setae; first maxilla palps with fewer apical teeth; second maxilla more slender; maxilliped palp article 3 more rugose, outer plate bearing mediofacial comb rows of robust setae, inner plate with fewer naked apical tooth like robust setae and more medial plumose setae; dactyls of gnathopods bearing more inner accessory spinules, second gnathopod dactyl with small recumbent inner tooth like robust seta; peraeopods 3 and 4, article 4 bearing small anterodistal rugose lobe; peraeopod 5 shorter and less spinose; peduncle of pleopod 1 without basolateral pubescence; urosomite one at the base of uropod 1 bearing a small rather than moderate to large articulated robust seta; telson cleft 40% rather than 50%, each lobe bearing three apical robust setae rather than one.

Distribution. Gurangah Cave, cave 321, Wombeyan cave system, New South Wales, 34°19'S 149°59'E.

Neoniphargus richardi n.sp.

Figs 42–45

Etymology. Named for the second son of the second author in recognition of his indirect contribution to amphipod studies.

Type locality. Among tree roots, River Cave Spring (Cave W47) Wombeyan Caves system New South Wales, 34°19'S 149°59'E.

Material examined. HOLOTYPE (Australian Museum P51376) female "a" 6.5 mm, ALLOTYPE (Australian Museum P51377) male "b" 5 mm, in the type series; one other female 6.5 mm, two juveniles 2.5 mm; collected by S. Eberhard; 16 March, 1993.

Diagnosis. Article 1 of the peduncle of first antenna longer than article 2; calceoli present on the second antenna of the male; mandibular palp article 2 longer than article 3, sparsely setose, setae of article 3 BCDE. Palmar corners of both gnathopods without special medial robust setae. Coxa 4 deeply emarginate in both sexes. Dactyls of peraeopods 3–7 with only one facial and one medial setule, legs 5–7 without fine setae except for an elongate basodactylar seta on each propodus, propodi bearing 4-4-1 posterior robust seta sets. Coxae 5–7 with only weak robust setae on the posterior lobe. Coxal gills present on legs 2–6. Epimera two and three with two and three ventro facial robust setae. Uropods with only short robust setae, the third uropod strongly extended posteriorly beyond the first and second in the whole animal, the peduncle 0.5× the length of the outer ramus, the outer ramus bearing robust setae arranged in multiples in several medial and lateral rows, without plumose medial setae, the second article short; the inner ramus with a single apical robust seta and without facial setae. The telson cleft about 50%, each lobe with single sub apical robust setae and paired lateral penicillate setules at M0.57.

Description of holotype (female "a"). *Body* (Fig. 42): weakly armed dorsally, pleonites 1–4 with few setae, pleonites 5 and 6 with two and three dorsal and dorso lateral strong robust setae, length 6.5 mm. *Head*: rostrum small, eyes absent, lateral cephalic lobes strongly projecting, antennal sinus moderate. *First antenna*: long, 0.5× the length of the body, 1.4× the second antenna, peduncles shorter than the flagellum, article 1 longest, ratio of lengths 30:25:16, calceoli and aesthetascs absent from the female, the accessory flagellum 2-articulate, extending to M0.9 of article 1 of the primary flagellum, primary flagellum of 17 sparsely setose articles—articles 3, 8 and 9 being longer. *Second antenna*: approximately 0.25× body length, peduncle longer than the flagellum—about 1.5×—peduncular articles 4 and 5 subequal, articles 3–5 with moderate ventral setation, the flagellum of nine articles, weakly setose ventrally, calceoli and aesthetascs absent from the female. *Left mandible* (Fig. 42): palp of three articles, the second longest, bearing eight inner marginal setae, the third weakly falcate, bearing 2B3C10D3E setae, rugose lobe on the mandible basal to the palp; incisor with five teeth, lacinia mobilis four teeth, accessory blades of three chisel robust setae and three plumose setae, molar bearing a moderate posterior pappose seta, with three brushy basal setae. *Right mandible* (Fig. 42): palp article 3 setae 2B3C10D3E, basal to the palp a rugose lobe; the incisor with four teeth, the lacinia mobilis bifid, denticulate on one face, four teeth and a cluster of fine basal setules on the other; accessory blades of two chisel robust setae and two plumose setae, with three brushy setae leading to the molar, molar triturative, with a long posterior pappose seta. *Maxillae* (Fig. 42): left first maxilla palp with four thin apical robust setae and two slender sub terminal facial setae, all armed with spinules or setules; outer plate with five denticulate terminal robust setae, and a small distomedial area of setules; inner plate bearing two plumose apical setae; right first maxilla palp second article with a mediodistal row of four naked tooth like robust setae, one distolateral armed robust seta and two slender facial setae; outer plate with five denticulate robust setae and two distomedial thin setae; inner plate bearing two plumose apical setae. Second maxilla: both plates with long curved distal setae; outer plate bearing a lateral sub apical short seta; inner plate with two distal mediofacial armed setae. *Maxilliped* (Fig. 42): palp third article with stout medial and facial setae and a group of three short and two small apicolateral setae, apex strongly produced and rugose, dactyl rugose and bearing three accessory spinules, the nail naked; inner plate with three apical naked tooth like robust setae, several plumose and naked setae and a medial marginal row of four plumose setae; outer plate bearing a distomedial to apical row of five progressively facial robust naked robust setae, an apical group of three slender armed setae, two ventrofacial short setae and a basomedial row of slender setae. *First gnathopod* (Fig. 43): coxal plate with sparse apical setae; articles 2–4 with small posterior rugose lobes; carpus short, strongly lobate, the lobe rounded, rugose, without apical setae; propodus trapezoidal, longer than wide, the posterior angle rounded and rugose, palmar corner bearing two medial and two lateral robust setae, palm transverse, slightly convex, palmar robust setae simple, dactylus with accessory spinules, and reaching to the palmar corner robust setae. *Second gnathopod* (Fig. 43): larger than the first; coxa sparsely setose apically, bearing simple sac like gill and broad long oostegite; articles 2–4 all bearing small posterior areas of rugosity;

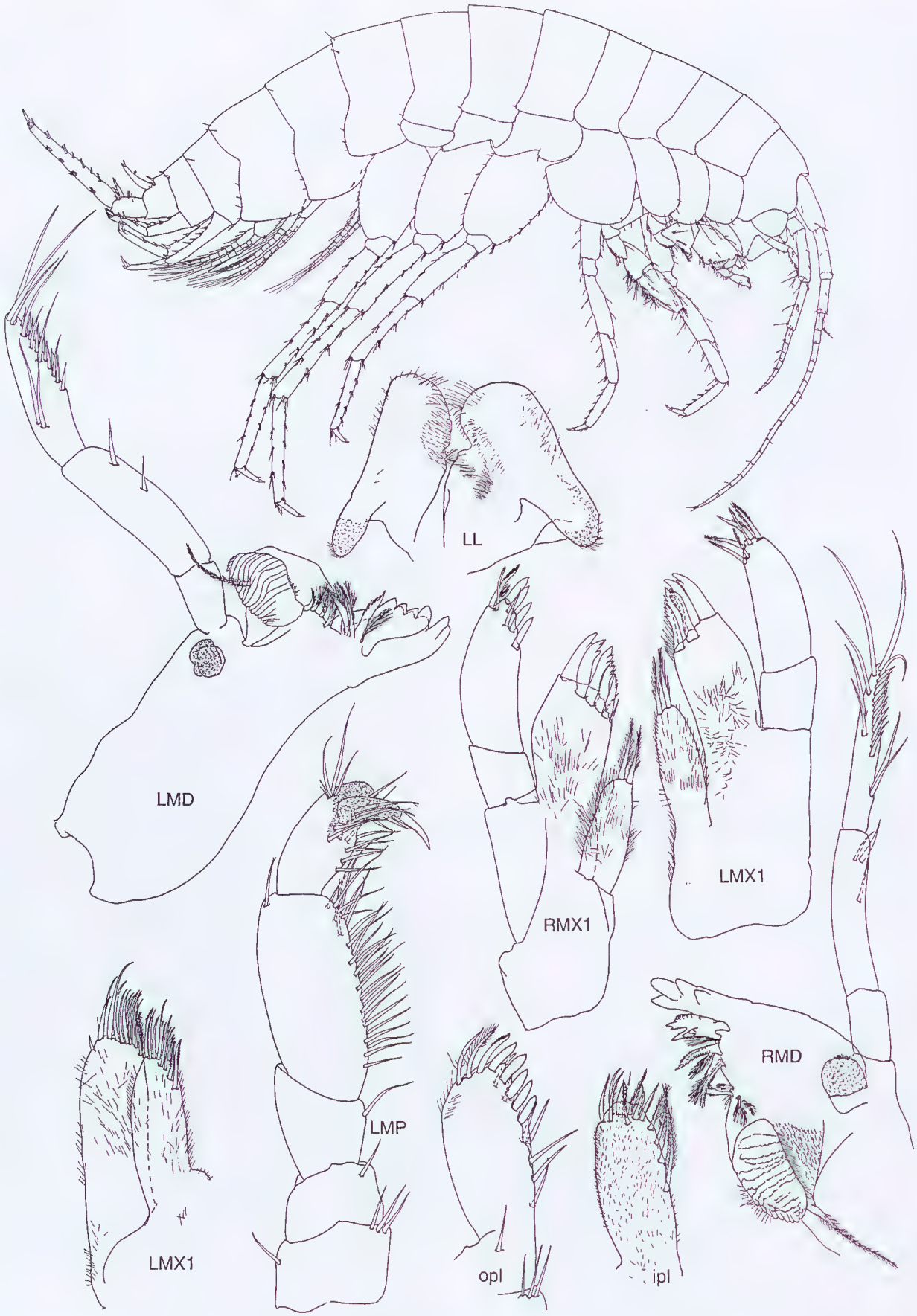

Fig. 42. *Neoniphargus richardi* n.sp. holotype female "a" 6.5 mm; whole, mouthparts.

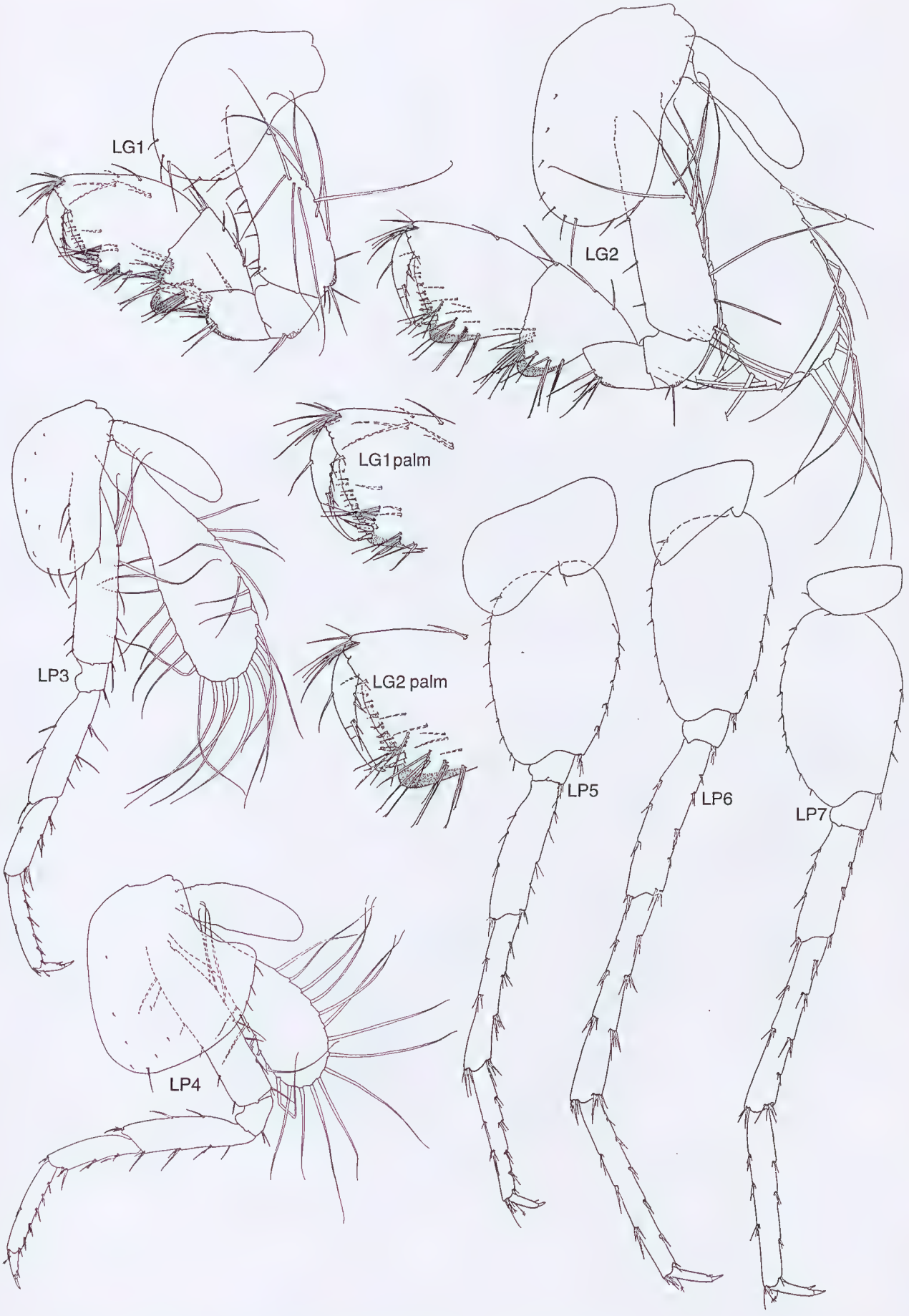

Fig. 43. *Neoniphargus richardi* n.sp. holotype female "a" 6.5 mm; legs.

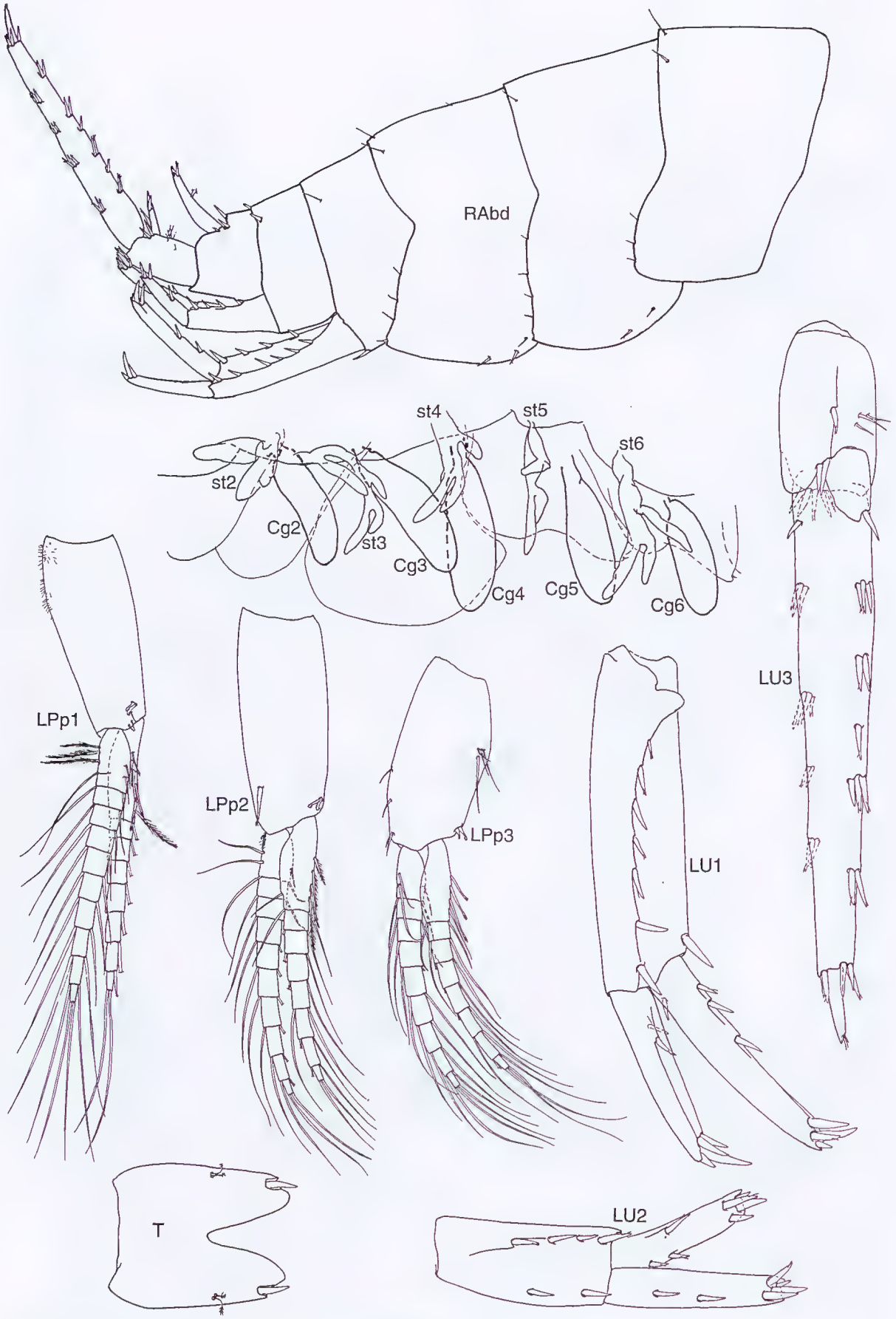

Fig. 44. *Neoniphargus richardi* n.sp. holotype female "a" 6.5 mm; abdomen, gills, pleopods, uropods, telson.

carpal lobe broader but not deeper than of the first gnathopod; propodus posterior corner lobate, larger than for the first gnathopod, rugose, the palmar corner with two lateral and one medial stout robust setae, dactylus reaching palmar corner robust setae. *Peraeopods* (Fig. 43): coxae 3 and 4 with few apical setae, coxa 4 moderately emarginate, both bearing simple sac like gill and broad, long oostegite; peraeopods 3 and 4 subequal in length, longer than the second gnathopod, articles 4 and 5 posteriorly spinose, posterior robust seta formulae of article 6 are 1-2-2-2-2 and 1-2-2-3-2 respectively; peraeopods 5–7 similar, leg six longest, coxae with 1-1-2 posterior weak robust setae, coxa 7 with no gill, articles 2 expanded posteriorly, weakly lobate post-ventrally, with small marginal setae, article 2 of peraeopod 6 slightly narrower; propodi with moderately long basodactylar setae. *Gills* (Fig. 44): coxae 2–6 bearing simple sac like gills; sternites 2–6 with pairs of fleshy, dendritic sternal gills attached to the posterolateral to mid lateral of each segment. *Epimera* (Fig. 44): second epimeron with a small post-ventral tooth, posterior margins of each convex to slightly sinuous bearing few setae, anterior ventro face of epimera two and three bearing two and three small robust setae. *Pleon*: few dorsal armaments; pleonites 5 and 6 with dorsal and dorsolateral robust setae; pleonite 6 bearing an additional robust seta basolateral to the telson. *Pleopods* (Fig. 44): similar, each with two retinacula; peduncle one with three small accessory setules, and short basolateral pubescence; peduncle two with a single distolateral strong seta; peduncle three with four lateral and four mid medial setae; rami of 10-8, 10-8, 9-8 articles respectively. *Uropods* (Fig. 44). Third uropod extending well beyond uropods 1 and 2 in the intact specimen; uropod lengths relative to uropod 1—uropod 2 0.7×, uropod 3 1.3×. First uropod: peduncle length 2.3× medial ramus, 2.9× lateral, lateral margin with a distal, subapical robust seta, and a dorsomarginal row of six short to moderate length robust setae, the mediodorsal face with a single subapical robust seta; rami unequal, outer ramus with one medial and one lateral robust seta and four apical robust setae; inner ramus with one basolateral robust seta, three medial robust setae and four apical robust setae. Second uropod: shorter than the first, peduncle bearing three dorsolateral and one subdistal short robust setae, and two medial robust setae; inner ramus longer than outer, with two medial robust setae and four apical robust setae; outer ramus with two medial, one lateral, and four apical robust setae. Third uropod: parviramous, peduncle length 0.3× length of the outer ramus, as long as urosomite three, bearing three dorsofacial robust setae, one mid medial and two medial robust setae basal to the inner ramus, and a distolateral row of five robust setae; outer ramus proximal article with four trans-lateral robust seta rows of 3-4-2-3 robust setae and five trans medial robust seta rows of 3-2-1-3-2 robust setae, two medial and three lateral distal robust setae basal to the second article; distal article bearing three small apical setules; inner ramus short, 0.13× outer ramus, with a single apical seta. Urosomite one at the base of uropod 1 bearing a moderate to large articulated robust seta. *Telson* (Fig. 44): short, about the same length as urosomite three, slightly longer than broad; cleft 50%; with a single subapical lateral robust seta on either lobe and paired dorsolateral penicillate setules on either lobe at M0.57.

Description of male "b". *Body*: length 5 mm. *First antenna* (Fig. 45): peduncle with sparse setae, relative lengths of articles 10:8:5, 0.5× flagellum length; accessory flagellum of two articles, small, reaching to M0.9 of first article of primary flagellum; primary flagellum long, of nineteen articles with sparse setae, aesthetascs present on articles 2–19. *Second antenna* (Fig. 45): short, 0.5× antenna one; peduncle 1.7× flagellum, articles 4 and 5 subequal, with sparse setation; flagellum of eight articles, moderately setate, calceoli present on articles 1–5. *Mandibular palp*: left palp article 3 setae 1B3C11D3E; right palp article 3 setae 2B4C12D3E. *First gnathopod* (Fig. 45): coxal plate with few apical setae and several small anterofacial setae; articles 2, 3 and 4 with small rugose posterior keels; carpus short, bearing a strong posterior rugose lobe; propodus with small rugose posterior keel; robust setae of palmar corner two medial, two lateral, palm slightly oblique and convex, palmar robust setae moderately crowded and simple; dactyl bearing three inner margin accessory robust setae, nail reaching to palmar corner robust setae. *Second gnathopod* (Fig. 45): coxa bearing sac like gill, with few apical or facial setae; articles 2–4 with tiny posterodistal rugose keel; carpus with prominent posterior rugose lobe; propodus with moderate to strong rugose posterior lobe, palmar corner with one medial and two lateral robust setae, palm slightly oblique, almost straight, palmar robust setae simple; dactyl with three inner margin accessory robust setae, nail reaching slightly beyond palmar corner robust setae. *Peraeopods* (Fig. 45): similar to female, except propodi of legs 5–7 with long basodactylar setae extending almost to or beyond the dactyl. *Epimera* (Fig. 45): without postventral teeth; with 0-2-3 ventrofacial robust setae; posterior margins convex, sinuous, and straight, all weakly setulate. *Pleon* (Fig. 45): pleonite 5 bearing a single dorsolateral robust seta; pleonite 6 with a dorsal robust seta basal to the telson. *Pleopods* (Fig. 45): peduncles each with two retinacula; third peduncle with a small distolateral slender seta and four setae on the mid posterior margin; rami with 5-9, 7-9, 5-8 medial and lateral articles respectively. *Uropods* (Fig. 45). First uropod: peduncle with four dorsolateral and one apicolateral robust seta, and three dorsomedial and one apicomedial robust seta; medial ramus with two lateral and four apical robust setae; lateral ramus with one lateral and four apical robust setae. Second uropod: peduncle with two laterodorsal and two apicolateral robust setae, and one apicomedial robust seta; medial ramus with one lateral, two medial and four apical robust setae; lateral ramus with one lateral and four apical robust setae. Third uropod: peduncle longer than urosomite three, bearing no marginal robust setae, and two apicolateral robust setae; inner ramus length 0.5× peduncle, 0.15× outer ramus, bearing one apical robust seta; outer ramus of two articles; proximal article length 5× distal, with transverse lateral robust seta rows of 2-2-2 and four distal robust setae, and transverse medial robust seta rows of 1-3-2-2 and one distal robust seta; distal article with one small apical setule. *Telson* (Fig. 45): longer than urosomite three; one apical robust seta on either lobe; lateral penicillate setules at M0.6 on either side.

Description of female "c" (6.5 mm), juveniles (2.5 mm.): essentially as for female "a".

Relationship. This species differs from others of the genus in the following ways: eyes absent; outer plate of first maxillae with five denticulate robust setae, rugosities absent from the posterior angle of article 4 of the second gnathopod of the male; palmar corner of first gnathopod with two or three robust setae rather than six or more; palmar robust setae not dense, or with triggers; the second article of peraeopods 5–7 least expanded on leg six rather than five; accessory seta

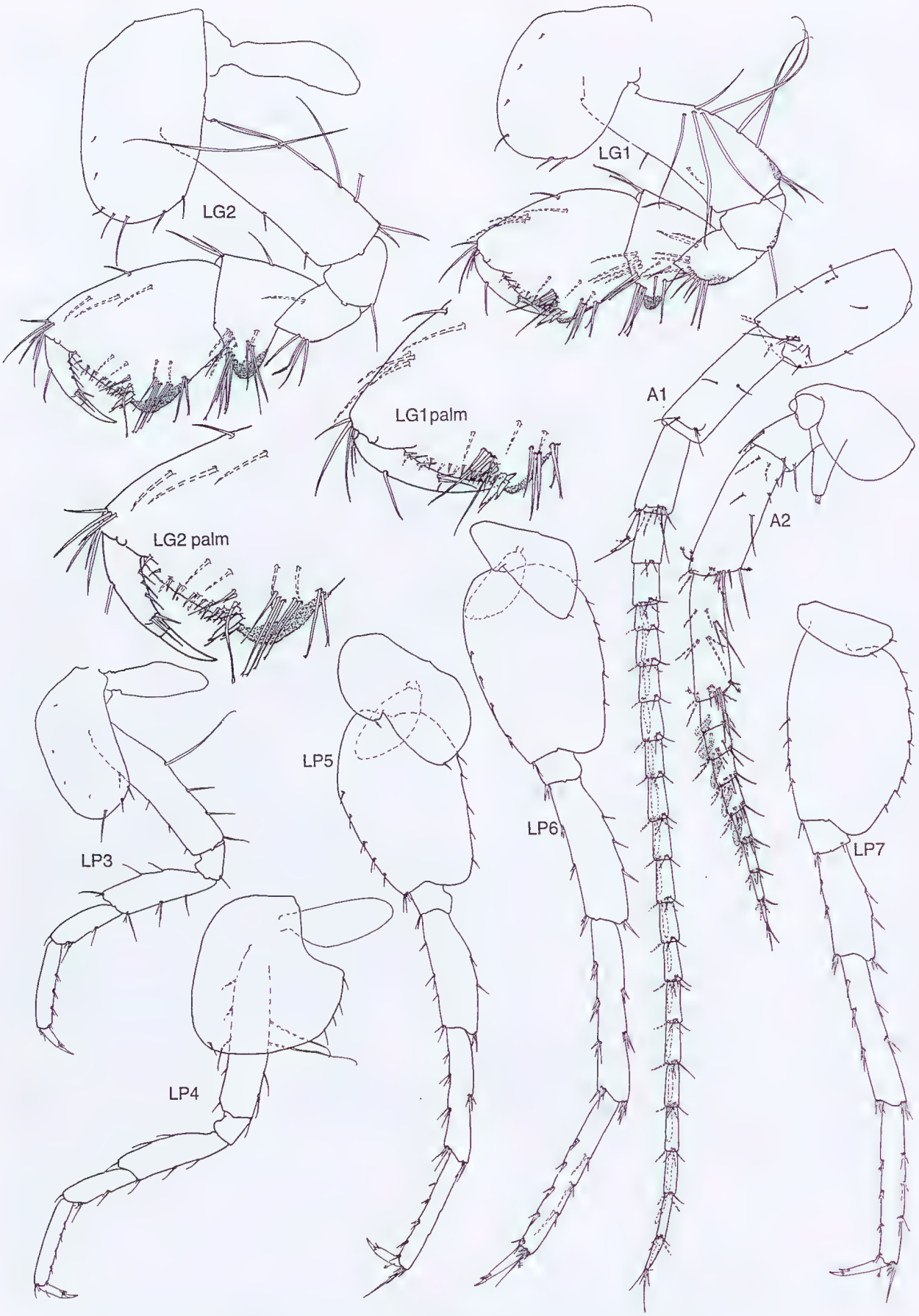

Fig. 45. *Neoniphargus richardi* n.sp. allotype male "b" 5.0 mm; antennae, legs.

present adjacent retinaculum of the first pleopod; one robust seta row on the inner ramus of uropod 2; setae absent from the inner margin of the ramus of uropod 3; telson cleft 50% rather than 60%.

Differences between *N. richardi*, and *N. coolemanensis* and *N. secus* are set out within discussion of those species.

Distribution. River Cave Spring, cave W47, Wombeyan cave system, New South Wales, 34°19'S 149°59'E.

Wesniphargus Williams & Barnard

Wesniphargus Williams & Barnard, 1988: 160–161

Type species. *Neoniphargus nichollsi* Straškraba, 1964.

Composition. This genus was monotypic, but we now add a further species, *W. yanchepensis*, from a cave in Western Australia.

Diagnosis. Williams & Barnard (1988) re-examined the incomplete holotype of *W. nichollsi* and provided both a generic diagnosis of *Wesniphargus* and a partial redescription of the type species, *W. nichollsi*, based on this examination and the original description and drawings of Straškraba (1964). Even so, the generic diagnosis was incomplete. The discovery of a further species that can be assigned unequivocally to the genus, and an examination of fresh material that can be assigned to *W. nichollsi*, permits completion of the generic diagnosis with some minor changes.

Pleonites with weak dorsal arms, rostrum small or obsolescent, lateral cephalic lobes weakly to moderately projecting, antennal sinus weak to moderate. Eyes present or absent. First antenna elongate, longer than second, ratio of peduncular articles 10:7:5 to 10:9:5, accessory flagellum 2-articulate. Second antenna flagellum length equal to or less than length of peduncle, with very large calceoli in male. Ratio of articles of mandibular palp 8:22:22 to 8:28:26, second article moderately setose, article 3 moderately to barely falcate, setae BCDE. Labium without inner lobes. Maxillae not medially setose on inner plates except in some one or two marginal plumose setae on the second; maxilla one inner plate sub rectangular with two apical plumose setae, the outer plate with seven robust setae, palps weakly asymmetric. Second maxilla inner plate lacking oblique row of facial setae, the apicomedial edge with one plumose medial seta. Maxillipedal palp article 3 with or without rugose apical lobe, marginally pubescent or bearing fine setae. Coxae 1–4 elongate, sparsely setose ventrally, coxae 1–3 lacking a row of posterior robust setae, coxa 1 subquadrate or tapering below, coxa 4 emarginate. coxa 5 much shorter than four. Gnathopods small; carpi shorter in male, lobate; articles 4 and 5 with or without rugosities; propodi not expanded apically, palms weakly oblique, lacking rugosities in some, robust setae symmetrically bifid or not, bearing short terminal triggers; robust setae at corner of palm four, with small sub apical triggers; robust setae along palm moderately dense, with or without triggers. Peraeopods 3 and 4, article 6, posterior robust seta sets evenly spaced, legs 5–7 moderately elongate, articles 2 of legs 5–7 broadly expanded, ovate, postventrally lobate. Dactyls of legs three to seven with one facial and one marginal setule. Gills borne on coxae 2–6, simple sac like, those of 5 and 6 slightly reduced in some. Thoracic segments 2–6 with lateral sternal gills of incipient dendritic form but fingers only small lumps. Pleopods; basomedial setae of inner rami bifid, branches dissimilar, of different length and shape, occasionally one branch of diamond head shape or both simple; two to four retinaculae each peduncle, with or without accessory retinaculae or robust setae. Epimera with small, blunt postventral extensions, but not forming teeth, some with facial robust setae, with or without setae near the ventral margin, posterior margins weakly setulate. Uropods: apicolateral corner of the peduncle of uropods 1 and 2 with one robust seta; outer rami of both uropods 1 and 2 shorter than the inner, the margins spinous; uropod 1 lacking basofacial arms. Uropod 3 extended, parviramous or magniramous and dispariramous, the peduncle short; outer ramus 2-articulate, medial setae moderately dense and plumose, article 2 short to very short; inner ramus short to aequiramous, sparsely setulate or with moderately dense plumose setae. Telson length moderate to elongate, cleft 75–85%, the lobes laterally tumid in some, with apical spination or both apical and dorsal robust setae, no major setation, no basolateral arms except for a pair of lateral penicillate setules at M0.6 to M0.7 on either side.

Additional Description. Upper lip uniform, rounded below. Accessory blades of mandibles with few interraker plumose setae, several to many additional setae beyond rakers onto the base of the molar, pappose posterior seta on either or both molars. Inner plates of maxillae weakly to moderately pubescent on inner margins. Maxilliped inner plate with distolateral row of one to three plumose setae, with additional robust setae and plumose setae; outer plate with a distal row of few plumose setae, with a medial submarginal row of blunt naked tooth like robust setae and facial robust setae; palp articles 2 and 3 poorly setose laterally, article 2 moderately to strongly setose medially, article 3 of some with a row of non comb robust setae near the base of the dactyl, the apex slightly produced, rugose in some, marginally pubescent or with fine setae. Gnathopod 1 without one seta of article 4 enlarged and robust seta like; dactyls without recumbent inner tooth like robust seta, with stiff spinules at the inner nail articulation, without additional spinules along the inner dactylar margin. Pleopods similar, peduncles naked, rami extending equally or subequally. Urosomite one with or without a robust seta of moderate length at the base of uropod 1.

Wesniphargus yanchepensis n.sp.

Figs 46–48

Etymology. Named for the type locality.

Type locality. Yanchep Cave, Western Australia, 31°33'S 115°41'E.

Material examined. HOLOTYPE (WAM 520-97) female "a", 8 mm, ALLOTYPE (WAM 521-97) male "b", 7 mm. Also in the type series: juvenile "c" 4 mm (WAM 522-97), Western Australian Museum, collected by W.F. Humphreys, M.S. Harvey, C. Rippon, from freshwater pool in limestone cave, with hand net, 19 April, 1991, Yanchep Caves, Western Australia, 31°33'S 115°41'E.

Diagnosis. Pleonites with weak dorsal arms. Head; rostrum obsolescent, lateral cephalic lobes moderately projecting, moderate antennal sinus. Antenna one elongate longer than second antenna, ratio of peduncular articles 4:3:2; accessory flagellum 2-articulate; second antenna flagellum length less

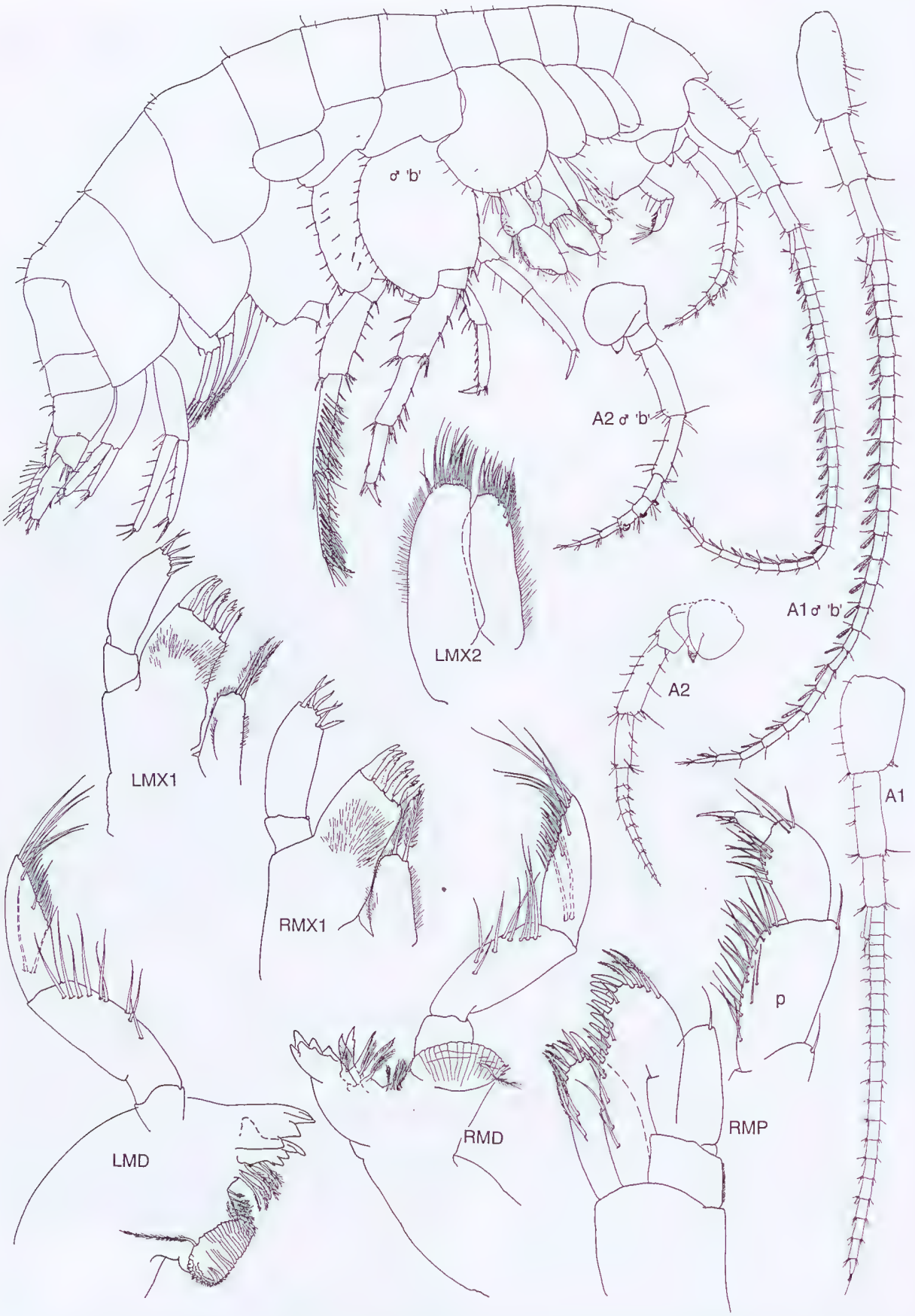

Fig. 46. *Wesniphargus yanchepensis* n.sp. holotype female "a" 8 mm; whole, antennae, mouthparts (all drawings except those indicated). Allotype male "b" 7 mm whole specimen, antennae.

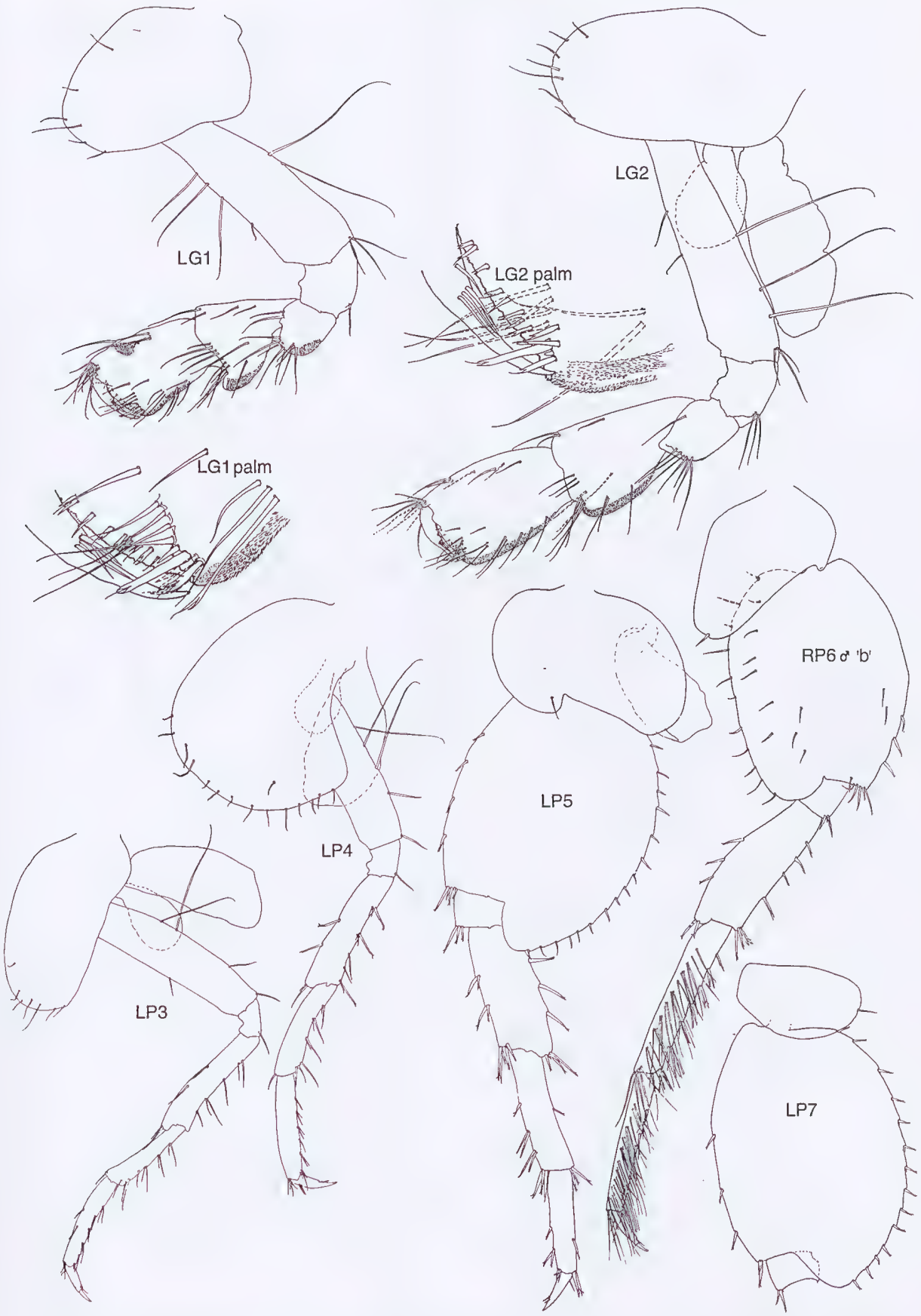

Fig. 47. *Wesniphargus yanchepensis* n.sp. holotype female "a" 8 mm; legs (all drawings except those indicated). Allotype male "b" 7 mm R peraeopod 6.

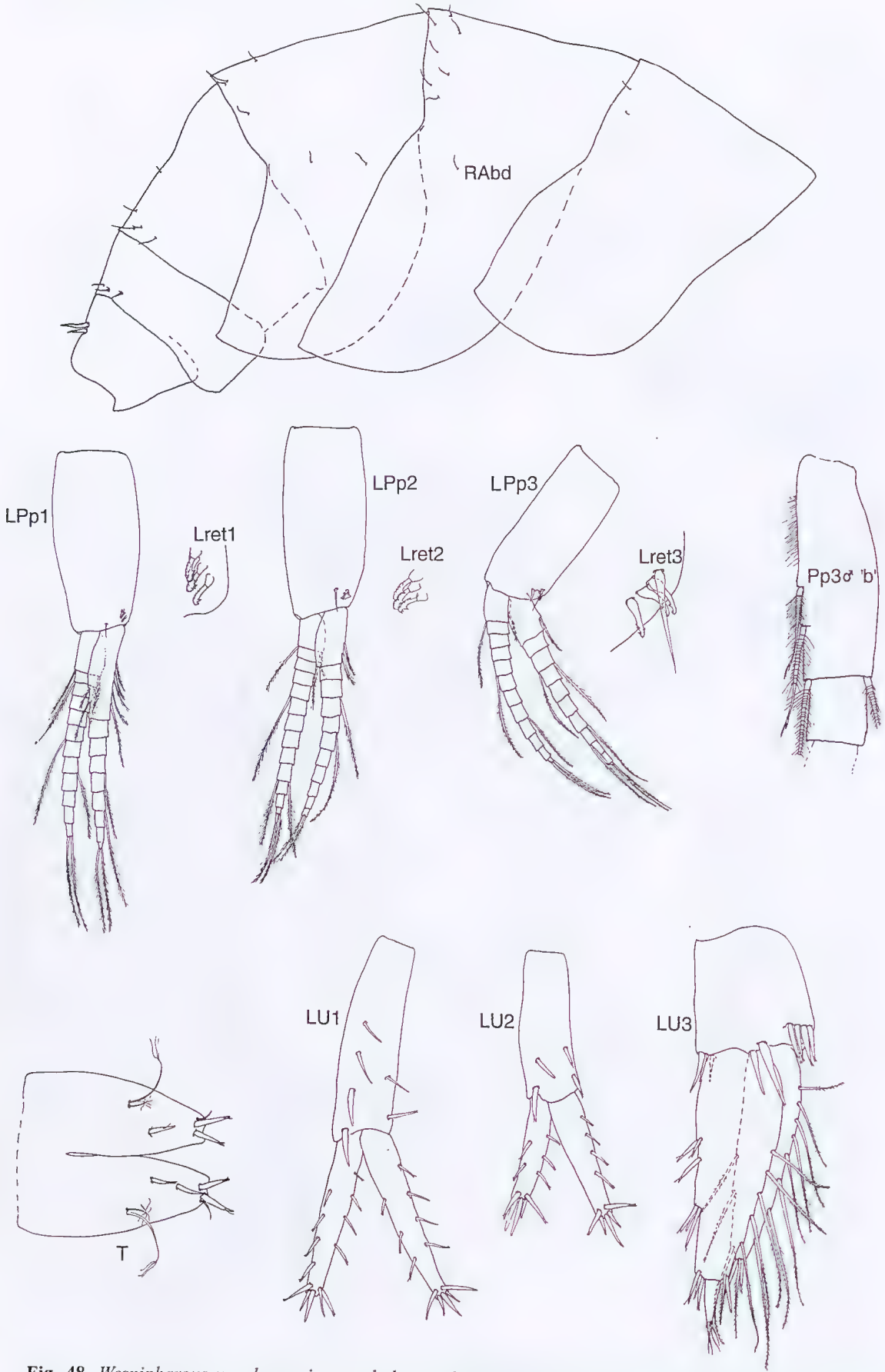

Fig. 48. *Wesniphargus yanchepensis* n.sp. holotype female "a" 8 mm; abdomen, gills, pleopods, uropods, telson (all drawings except those indicated). Allotype male "b" 7 mm articles 1 and 2 inner ramus, pleopod 3.

than peduncle. Mandibular palp ratio of articles 7:25:23; article 2 moderately setose, article 3 barely falcate, setae BCDE. Labium with no inner lobes. Maxillae not medially setose on inner plates except for two marginal plumose setae on second maxilla at M0.8; first maxilla inner plate sub rectangular, with two apical plumose setae; outer plate with seven denticulate robust setae, palps almost symmetric—left side with thin apical robust setae, right palp with mix of stout and slender robust setae. Second maxilla: inner plate lacking an oblique row of setae on the face, apicomedial margin with two plumose medial setae. Maxilliped: palp article 3 with a slight apical lobe bearing fine marginal setules. Coxae 1–4 elongate, sparsely setose ventrally; coxae 1–3 lacking a row of posterior robust setae; coxa 1 tapering below; coxa 4 emarginate; coxa 5 shorter than coxa 4. Gnathopods small, not sexually dimorphic in the palmar spination, carpi longer in female (0.7–0.8× propodi), lobate; articles 4–6 of gnathopods bearing post-marginal rugosities; article 4 of gnathopod 1 bearing a rugose margin; propodi not expanded apically; palms weakly oblique and convex; robust setae symmetrically bifid, also bearing short terminal triggers; robust setae at corner of palm two long and two short, bifid and with small triggers; robust setae along palm moderately dense with triggers on most. Gnathopod 1: propodus posterior margin arms of a single robust seta in tandem, with an additional submarginal transverse row of three robust setae at M0.5. Peraeopods 3 and 4 article 6 with posterior robust seta sets evenly spaced; peraeopods 5–7 moderately elongate; article 2 broadly expanded, ovate, postventrally lobate; peraeopods 3–7 dactyls with one marginal and one facial setule. Oostegites present on female coxae 2–4. Coxae 2–6 with sac like gills; gills 5 and 6 not reduced. Thoracic segments 2–6 with lateral sternal gills; small, lumpy, but not dendritic. Pleopods 1–3 with basomedial setae, bifid, branches dissimilar, of differing length and shape, some with one branch of diamond head, this organ borne at about M0.5 of the branch; retinaculae 4-3-3 respectively, accessory retinaculae 0-1-1. Epimera: post-ventrally bearing very small rounded extensions: blunt, without a tooth; none with facial robust setae, without setae near the ventral margin; posterior margins weakly setulate. Uropods; apicolateral corner of peduncle of uropods 1 and 2 with one robust seta, with a pair of mediomarginal robust setae at M0.7, and at M0.9; outer rami shorter than inner, margins spinose; uropod 1 lacking basofacial arms; all rami with two robust seta rows; uropod 3 extended, magniramous, dispariramous, peduncle short, outer ramus lanceolate, 2-articulate, medial setae moderately dense and plumose; article 2 very short, inner ramus dispariramous, lanceolate, with moderately dense plumose medial setae. Telson of moderate length; cleft 75%; lobes moderately tumid laterally, with apical and dorsal spination; no major setation; no basolateral arms, except for a pair of lateral penicillate setules at M0.6 on the dorsolateral face.

Additional characters. Upper lip uniformly rounded below; accessory blades (rakers) usually with few interraker plumose setae; many additional (penicillate) setae beyond rakers onto base of molar; large basal ragged molarial seta on R mandible; no other apical molarial seta. Lower lip uniform, inner lobes absent; medial margins of inner plates of maxillae moderately pubescent, both plates with long apical setae; inner plate with three distal plumose setae, apical robust setae and mid-facial plumose setae; outer plate with a distal row of plumose setae, medial submarginal teeth and facial robust setae; palp articles 2 and 3 poorly setose laterally, basally naked; article 2 strongly setose medially, article 3 without a row of non comb robust setae near the dactylar base, apex only slightly produced, not rugose, marginally pubescent or with fine setae. Dactyls without small recumbent inner tooth like robust seta on either gnathopod, with stiff spinules or setules at inner nail articulation line, without additional spinules along inner dactylar margin. First gnathopod without seta of the fourth article enlarged and scythe like. Pleopods similar, peduncles naked, rami extending equally. Urosomite one, at the base of uropod 1 without a robust seta.

Description of holotype (female "a"). *Body* (Fig. 46): pleon sparsely armed dorsally, few setae on pleonites 1–5; moderately setose distolaterally, pleonite 5 without robust setae on each side, pleon six with a pair of dorsolateral robust setae each side, length 8 mm. *Head*: rostrum absent, eyes absent. *First antenna* (Fig. 46): length 0.46× body, 1.8× second antenna; peduncle much shorter than flagellum, ratio of lengths of articles 21:18:11 (= 3.8:3.2:2), flagellum of 22 articles, without aesthetascs or calceoli; articles not uniform, proximal articles 3–6 shorter than distal articles, article 3 shortest; sparsely setulate; accessory flagellum 2-articulate, extending to M0.6 of article 3 of the primary flagellum. *Second antenna* (Fig. 46): length 0.25× body, flagellum of nine articles, the peduncle longer than the flagellum; article 4 longer than five, articles 3–5 with sparse ventral setation, without calceoli or aesthetascs. *Upper lip*: apical margin evenly rounded. *Left mandible* (Fig. 46): ratio of lengths of palp articles 8:28:26, article 2 with nine long naked medial to distofacial setae, article 3 without pubescence, setae 2B2C14D5E; incisor with four teeth; lacinia four large and one small teeth; three setose accessory blades and three plumose interraker setae, a row of plumose setules leading to base of the molar; molar bearing posterior pappose seta, without other penicillate basal setae. *Right mandible* (Fig. 46): incisor with two rows of cusps of four large and three small teeth; lacinia mobilis bifid, both blades acuminate, the medial blade with a medial marginal pair of small teeth at M0.75, the lateral blade bearing weak facial cusps and a row of setae; accessory blades of two rakers and two plumose robust setae; palp article 2 bearing nine facial setae; setae of palp article 3 2B2C13D6E; molar bearing large posterior pappose seta. *Lower lip*: without inner lobes; bearing slender robust setae apically on outer lobes; facially and marginally pubescent; posterior protuberances also marginally pubescent. *Maxillae* (Fig. 46). Left first maxilla: palp article 2 with five thin apical robust setae and one mediodistal robust seta, without other setae; outer plate with seven robust setae, most denticulate, facially pubescent; inner plate with two apical plumose setae borne on the distomedial margin, outer distal and inner margins pubescent, with a mid-facial row of pubescence. Right first maxilla: palp article 2 bearing four slender terminal robust setae and two mediodistal robust setae, one armed on the medial margin with short setules, the other naked, slender; outer plate bearing seven denticulate terminal robust setae, facially pubescent; inner plate with two apical plumose setae, borne on the medial margin; medial and lateral margins as well as a small laterofacial area pubescent. Second maxillae: similar; most robust setae of both plates long, curved; outer plate apex bearing many long, curved robust setae, lateral margins pubescent; inner plate subapical medial corner bearing a short row of plumose setae, apex bearing many long, curved setae; medial margin pubescent. *Maxilliped* (Fig. 46): palp laterally pubescent basally, articles 2 and 3 poorly setose laterally, article 2 strongly setose medially, article 3 without comb robust setae basal to the dactyl, the apex slightly produced bearing a few short marginal setules, and a transverse subapical facial row of three long setae; inner plate bearing three distal plumose setae, four apical stout naked robust setae, two medial subapical robust setae and two facial

plumose setae at M0.4 and M0.6; outer plate bearing a distolateral row of four plumose setae, a submarginal medial row of eight naked tooth like robust setae extending from M0.6 to the mid apex, the medial margin thus robust setae absent beyond M0.6, a discontiguous mediofacial row of eight slender robust setae extending from M0.2 to M0.9 and two slender medial robust setae at M0.4 and M0.55. *First gnathopod* (Fig. 47): coxal plate with four slender apical and three facial anterior setae; articles 2 and 3 without rugosities; article 4 with small posterior rugose hump; carpus short, lobate—lobe tilted apically—and rugose; propodus sub rectangular, slightly expanded apically, longer than wide, length to width ratio; 48:33, bearing an anterior facial area of rugosities, palmar corner rounded, with a narrow rugose posterior keel, the corner marked by two medial and two lateral bifid robust setae which also bear short triggers; one lateral robust seta slightly elongate; palm weakly oblique, slightly convex, dactylus without recumbent inner tooth like robust seta, reaching end of palm. *Second gnathopod* (Fig. 47): coxa moderately setose apically, bearing sac like gill and long naked oostegite; articles 2 and 3 without posterior rugosities, article 4 with a small rugose keel; carpus longer than gnathopod 1, with a long rugose posterior lobe; propodus longer and narrower than on gnathopod 1, length to width ratio; 80:130; posterior margin a long rugose keel; palmar corner rounded, marked by four lateral robust setae; dactyl bearing three stiff setules at inner nail articulation line and a single, more proximal robust seta, reaching slightly beyond the robust setae of the palmar corner. *Peraeopods* (Fig. 47): coxa 3 with six apical setae as well as a single anterior seta; coxa 4 emarginate, ventrally and post-ventrally bearing fourteen setae and one ventrofacial seta; peraeopods 3 and 4 weakly setose posteriorly, three less setate than four; articles 6 and 7 post-marginal robust seta formulae 3-2-2-2-1 plus two locking robust setae and 1-2-2-1-2 plus three locking robust setae, respectively; peraeopod 5 article 6 with few posterior robust setae; peraeopod 6 articles 5 and 6 with many robust setae and setae; peraeopods 3–7 dactyls with one medial and one facial setules; coxa 5 only with a single ventromarginal robust seta; coxae 6 and 7 naked ventrally with a single post-ventral robust seta at the posterior corner, coxa 7 also with a single posterior robust seta; article 2 broadly expanded, ovate, lobate postventrally, with short to moderate posterior setules. *Gills* (Fig. 48): coxae 2–6 with sac like gills, 5 and 6 not reduced; sternites 2–6 with pairs of fleshy sternal gills bearing small lumps, of incipient dendritic form, attached between centre and lateral edge of each segment. *Oostegites* (Fig. 47): present on female coxae 2–5, broadly ovate on coxae 2–4, more slender on coxa 5; margins without elongate setae. *Epimera* (Fig. 48): 1–3 without postventral teeth; each with a small blunt protrusion, not acuminate, smallest on epimera three; posterior margins almost straight, without ventral robust setae, adjacent each post-ventral margin a single seta dorsal to the margin. *Pleon* (Fig. 48): with few dorsal setae or robust setae; dorsolateral posterior margin of pleonites 1–6 with setae: 6-11-9-6-4-0, and robust setae: 0-0-0-0-0-2. *Pleopods* (Fig. 48): similar, without peduncular arms, with 4-3-3 retinacula and an associated or accessory robust seta; basal setae of inner ramus bifid with similar and dissimilar branches, rami of 12-9, 13-11, 12-11 articles respectively. *Uropods* (Fig. 48). Uropod 3 extending beyond uropods 1 and 2 in entire animal. Uropod lengths relative to uropod 1; uropod 2 0.65×, uropod 3 1.1×; most robust setae of uropods bearing short subdistal triggers. First uropod: peduncle length 1.1× inner ramus, 1.1× outer ramus; outer margin without apical robust seta, and with weak row of four dorsolateral robust setae, the most distal being medio-subapical; medially 2 weak robust setae; the lateral ramus slightly shorter than medial (35:37); both with two rows of marginal robust setae, both apices with five terminal robust setae. Second uropod: peduncle about 1.2× length of inner ramus, with two medial and two lateral dorsal robust setae; outer ramus shorter than inner (22:26), with two rows marginal robust setae; inner ramus without a lateral row of robust setae; apices of both rami with five terminal robust setae. Third uropod: peduncle length 0.5× length of first article of outer ramus, 0.75× urosomite three, with a subdistal medial transverse row of four trigger robust setae, a pair of apicodorsal robust setae, two dorsal and one ventral apicolateral robust setae; outer ramus proximal article with four lateral trigger robust seta clusters: discontiguous; lateral robust setae proximal to distal 0-2-1-0-3-0-3; medial margin with six plumose setae and one distal robust seta; distal article small, much shorter than proximal (28:133); apex with four sub terminal dorsal short stiff setae; inner ramus length approximately 0.7× length of outer ramus, bearing on the inner margin a row of eight plumose setae; outer margin with three plumose setae; apex with one plumose seta and two trigger robust setae. *Telson* (Fig. 48): moderately long, 1.2× length urosomite three; cleft 75% of length; lobes moderately tumid laterally; apex notched, both apices blunt, rounded; dorsal subapices each with two large robust setae and a small lateral penicillate setule; a single dorsal robust seta on the right lobe at M0.7, two dorsal robust setae on the left lobe at M0.7 and M0.8; each lobe with a pair of penicillate setules dorsolaterally at M0.6.

Description of allotype (male "b"). Similar to female except in the following. *Body*: length 7 mm. *First antenna* (Fig. 46): length 0.67× body, 2.5× second antenna; ratio of lengths of peduncular articles 4:2.5:2; flagellum of 27 articles all except basal and ultimate article with aesthetascs; calceoli absent. *Second antenna* (Fig. 46): 0.26× body length, flagellum of six articles, without aesthetascs, articles 1–3 bearing large type nine calceoli. *Mandibles*: left palp article 2 with five moderate mediodistal setae, article 3 with setae 1B2C9D4E; right palp article 2 with five moderate mediodistal setae, article 3 with setae 2B2C10D4E. *Gnathopods*: carpi short, about 0.5× propodi. *Pleon*: pleonites 5 and 6 with two distolateral robust setae. *Pleopods* (Fig. 48): peduncles each with two retinacula, one and three with a single small mediodistal robust seta; rami with 6-9, 8-9, 7-10 medial and lateral articles respectively, inner setae of first article of medial ramus apically bifid. *Uropods*: peduncle of uropod 1 with three dorsolateral and two dorsomedial robust setae, margins each with one apical robust seta, outer ramus with three medial, two lateral and five apical robust setae, inner ramus with two medial one lateral and five apical robust setae; peduncle of second uropod with one dorsomedial and one apical robust seta one each side, outer ramus with one lateral, two medial and five apical robust setae, inner ramus with two lateral, two medial and five apical robust setae. *Telson*: slightly longer than urosomite six; two apical robust setae on either lobe plus a dorsal robust seta on each at M0.75, and a pair of lateral penicillate setules at M0.6.

Description of juvenile "c". *Body*: length 4 mm. Similar to female "a".

Relationship. *Wesniphargus yanchepensis* differs from *Wesniphargus nichollsi* in: eyes absent; flagellum of first and second antennae with more articles; flagellum of first antenna with paired aesthetascs on several articles; second article of mandibular palp relatively shorter; third article of mandibular palp without pubescence, bearing

more E setae; lower lip posteriorly pubescent; palps of first maxilla with fewer setae, and outer plate facially pubescent; third article of maxillipedal palp without rugosities, outer and inner plates bearing more setae; propodi of both gnathopods bearing rugosities; carpus of second gnathopod long; coxae of peraeopods 5–7 each bearing a post-ventral robust seta; peraeopod 6, articles 5 and 6 bearing many setae; coxal gills 5 and 6 not reduced; epimera without post-ventral teeth; pleopods bearing 4-3-3 retinacula (cf. two each); third uropod aequiramous, and bearing medial setae; telson broader and bearing dorsal robust setae additional to paired apical robust setae.

Distribution. Yanchep Cave, Western Australia, 31°33'S 115°41'E.

Wesniphargus nichollsi (Straškraba)

Figs 49–53

Diagnosis. As set out by Williams & Barnard, 1988

Description. As described by Williams & Barnard, 1988.

Material Examined. Western Australian Museum: female "a", 5 mm (WAM 523-97) and male "b", 2.8 mm (WAM 524-97), outflow of Mammoth Cave, Western Australia, 34°03'S 115°01'E; male "d", 2.8 mm (WAM 525-97), from a pool of black water beside the Yellingup to Augusta Road near Margaret River, Western Australia, 33°54'S 115°20'E; all collected by K. Davies, C.M. Austin, B. Knott on 29 August, 1991. This material can be assigned without equivocation to the taxon *W. nichollsi*: it conforms in all essential features to the redescription of this taxon provided by Williams & Barnard (1988). Given the incomplete nature of that redescription (see above), and the provenance of some of the fresh material, the opportunity is taken to fully describe this fresh material.

Description of male "b". *Body*: pleon sparsely armed dorsally; pleonites 1–4 moderately setose distolaterally; pleonite 5 with four lateral robust setae; pleonite 6 with two lateral robust setae; length 2.8 mm. *Head*: rostrum absent; eyes large, dark, reniform *First antenna* (Fig. 49): length 0.45× body, 1.8× antenna two, peduncle much shorter than flagellum, ratio of lengths of articles 10:7:5, flagellum of fifteen articles, without calceoli, articles 3–11 and 14–15 each with one aesthetasc, articles not uniform, proximal articles shorter than distal, article 3 shortest; accessory flagellum 2-articulate, extending to M0.5 of the second article of the primary flagellum. *Second antenna* (Fig. 49): length 0.25× body; peduncle longer than flagellum, article 4 longer than five, articles 3–5 with sparse ventral setation; left flagellum 6-articulate, right five, weakly setose ventrally, bearing giant calceoli on articles 1–4 of the left flagellum, articles 1–3 of the right, and distal aesthetascs on antepenultimate and ultimate articles of each *Upper lip*: apical margin rounded evenly. *Left mandible* (Fig. 49): palp article 3 shorter than 2, ratio of lengths 8:35:20, article 2 with long ventrofacial setae and mid-marginal pubescence; article 3 short, falcate, ventrobasally pubescent, setae 0C6D6E; incisor six toothed; lacinia mobilis with five teeth; three setose accessory blades and two plumose interraker setae, several brushy setae onto the base of the molar. *Right mandible* (Fig. 49): ratio of palp article lengths 8:25:20, article 2 ventromedially and facially pubescent, bearing two medial marginal and five submarginal to facial long setae; incisor with four teeth, lacinia mobilis bifid, the anterior branch with 11 peg like, terminally rounded denticles and terminating in a tooth, the posterior branch with seven peg like denticles; accessory blades of two rakers and plumose setae; molar strongly triturative with posterior pappose seta. *Lower lip* (Fig. 49): without inner lobes, bearing elongate blunt robust setae apically on the outer lobes, facially and marginally pubescent; posterior protuberances marginally pubescent. *Maxillae* (Fig. 49). Left first maxilla: palp article 2 narrow, with five thin apical robust setae and two sub apical facial setae; outer plate with seven strong denticulate robust setae; inner plate with two plumose apical setae. Right first maxilla: palp article 2 broad with one apicolateral long stout robust seta distomarginally setulose, two subterminal facial setae, one armed, two stout naked distal robust setae and one small distomedial robust seta; outer plate bearing seven denticulate terminal robust setae; inner plate with two apical plumose setae. Second maxilla: with long distally curved, blunt and flattened apical setae; outer plate mediolateral submarginal face with a short row of two or three long robust setae; inner plate distomedial corner with a slightly submarginal thick plumose seta. *Maxilliped* (Fig. 49). Palp: article 3 with several thick setae on the inner edge, two ventral submarginal setae, a row of four robust setae basal to the dactyl and the adjacent margin pubescent, three strong distolateral robust setae, the apex weakly produced and rugose; dactyl unguiform with a nail, and two accessory marginal spinules; article 2 well setose medially. Inner plate: bearing three stout naked apical robust setae, a short discontinuous row of three plumose submarginal facial setae extending apically from M0.6, and facially distolaterally a single plumose seta and a naked robust seta. Outer plate: with three slightly submarginal mediodistal naked tooth like robust setae, one apical naked tooth like robust seta and three distolateral pappose robust setae. *First gnathopod* (Fig. 50): coxal plate with few apical setae; articles 3–5 with posterior rugose lobes, small on article 3, moderate on articles 4 and 5; carpus short; propodus sub rectangular—length to width ratio 92:65—not expanded apically, palmar corner sub rectangular, not rugose, with two medial and two lateral naked blunt robust setae, palm very weakly oblique, slightly convex, dactylus without accessory marginal spinules, nail long, reaching to palmar corner. *Second gnathopod* (Fig. 50): coxal plate poorly setose apically with three long and three short setae, bearing a long simple sac like gill; articles 2–4 with small posterior rugose margins, carpus longer than the first gnathopod, the lobe much reduced; propodus longer and narrower than the first—length to width ratio 92:50—palmar corner three lateral and one medial stout robust setae, palm with moderately dense simple robust setae. *Peraeopods* (Figs 50, 52): coxa 3 with three long and six short apical setae and a facioanterior row of four moderate setae; coxa 4 emarginate, moderately setose apically and facially; peraeopods 3 and 4 weakly spinose posteriorly, articles 6 with posterior robust setae 1-1-1-1 and 1-1-2-2 plus two locking robust setae, respectively; posterior lobes of coxae of peraeopods 5–7 dominant, with few ventromarginal robust setae (1-1-2), articles 2 strongly expanded, very broadly lobate postventrally, with short posterior setules. *Gills*: coxae 2–6 with sac like gills, those of 5 and 6 reduced slightly; sternites 2–6 with pairs of fleshy lumped gills attached to the lateral edge of each segment. *Epimera*: postventral teeth small blunt protrusions, not acuminate, smallest on the third; posterior margins almost straight; second epimeron with three anteroventral submarginal robust setae, the third with two. *Pleon*: with few dorsal setae and robust setae; pleonites 1–6 with setae 9-6-9-4-0-0, pleonites 5 and 6 with 4-2

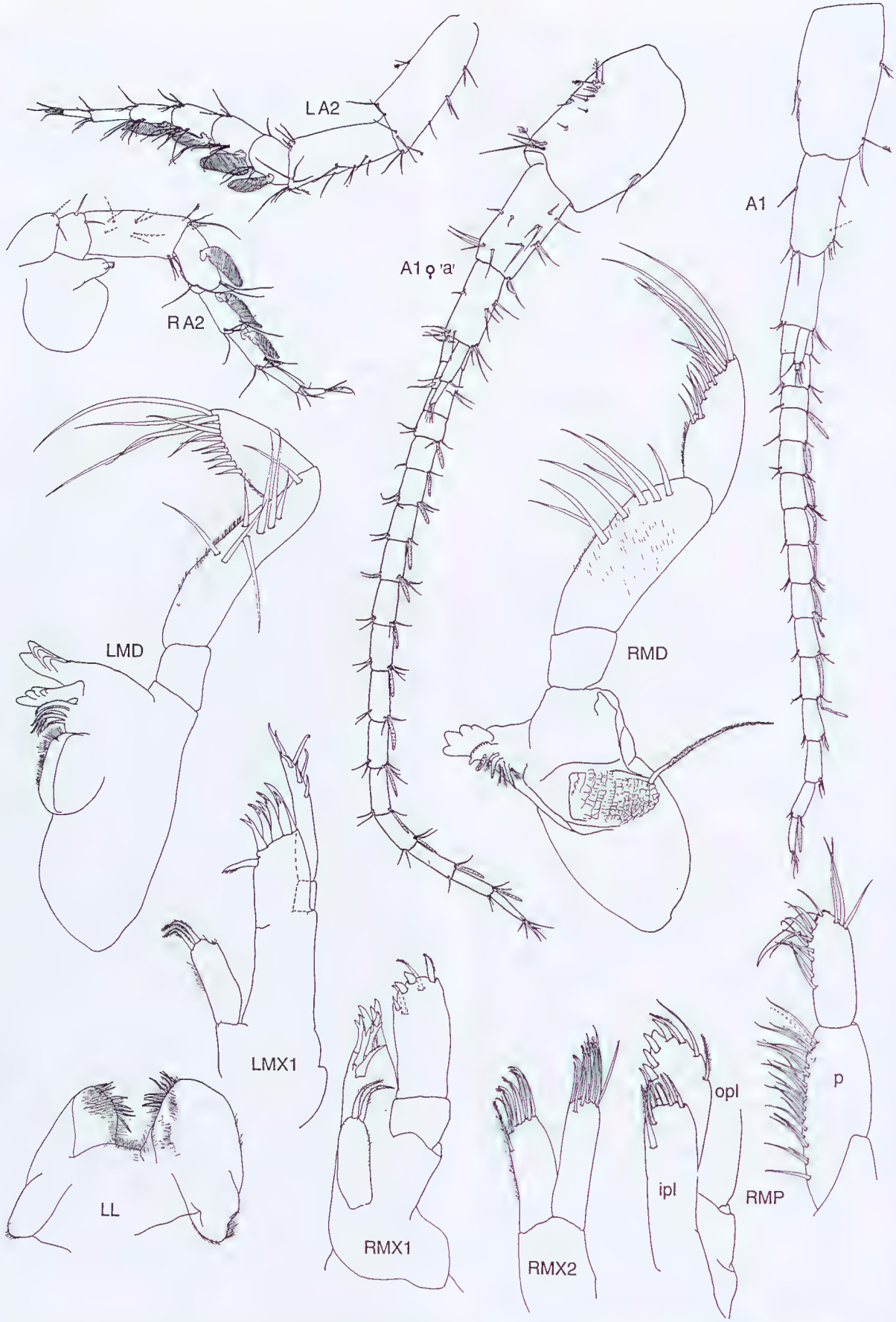

Fig. 49. *Wesniphargus nichollsi* (Straškraba) male "b" 2.8 mm; antennae, mouthparts(all drawings except those indicated). Female "a" 5.0 mm first antenna.

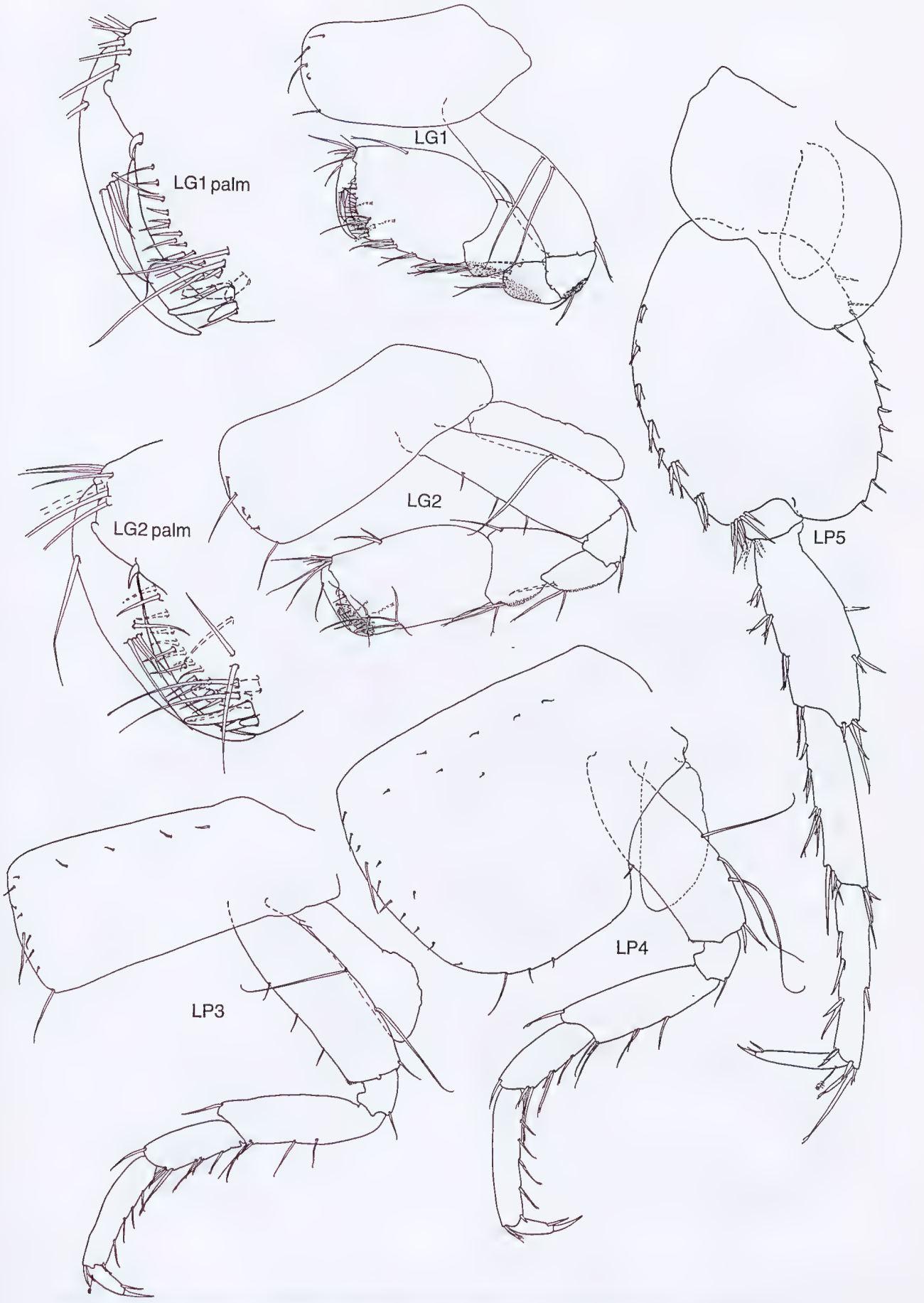

Fig. 50. *Wesniphargus nichollsi* (Straškraba) male "b" 2.8 mm; gnathopods.

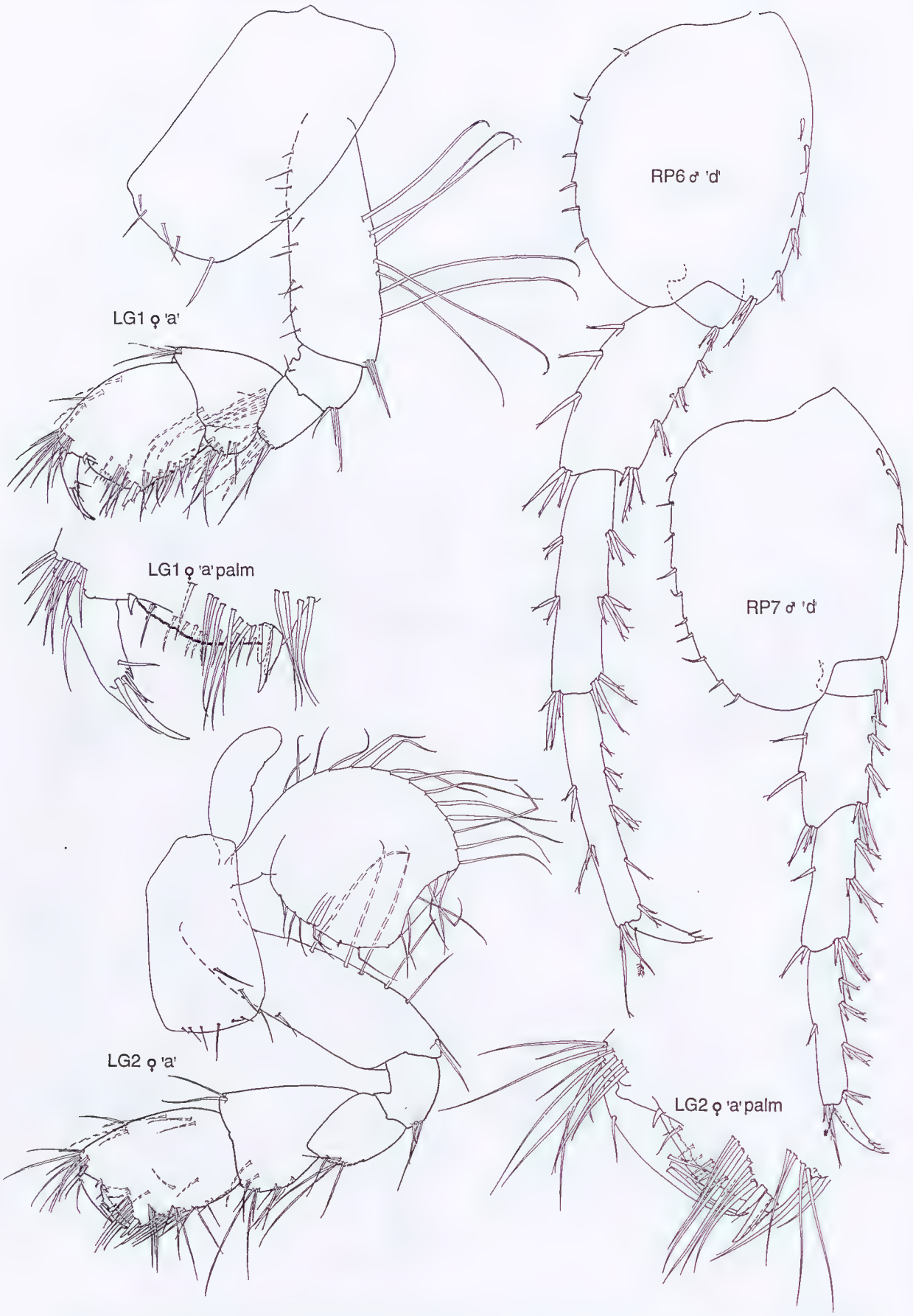

Fig. 51. *Wesniphargus nichollsi* (Straškraba) female "a" 5.0 mm gnathopods 1 and 2, male "d" right peraeopods 6 and 7.

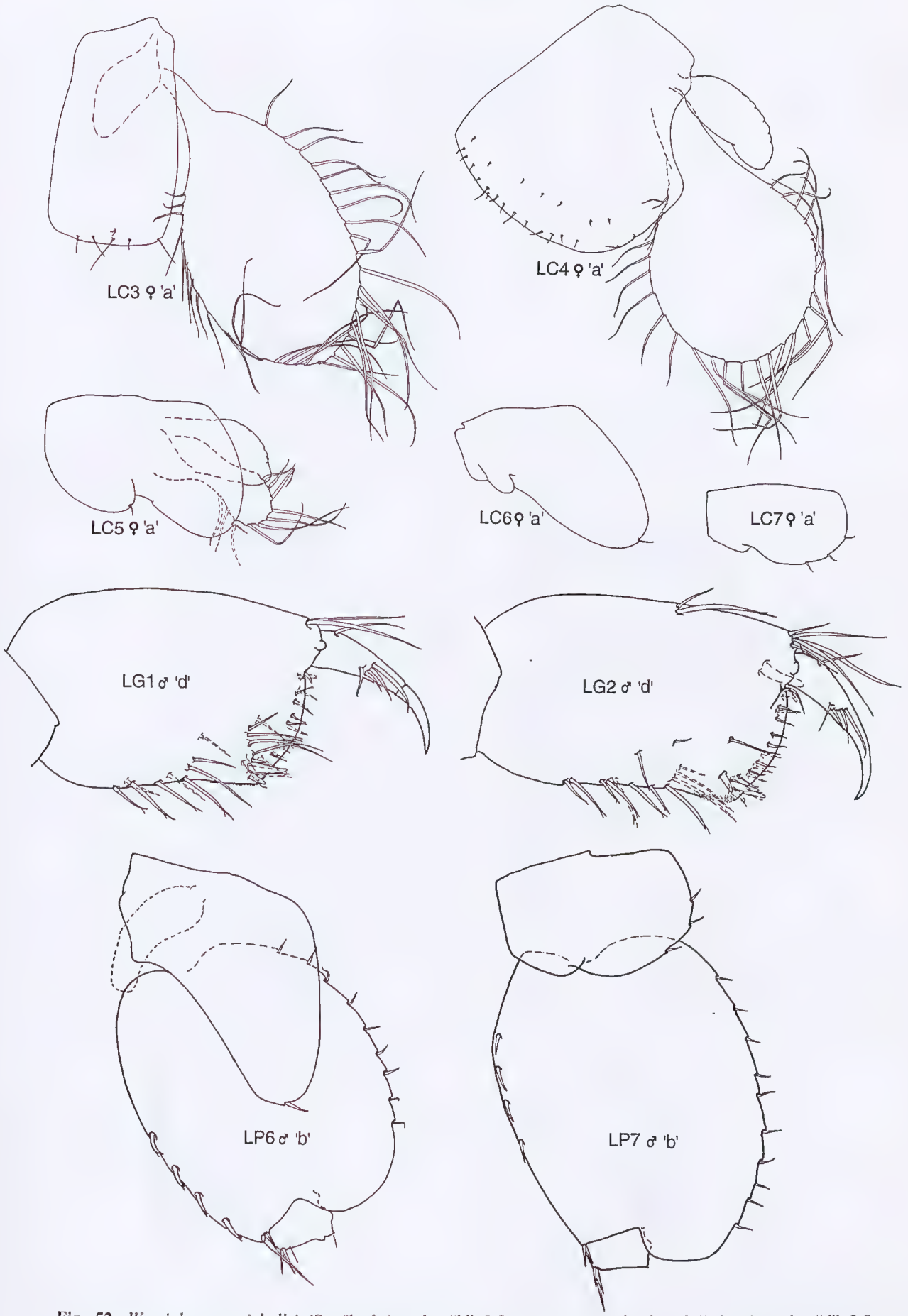

Fig. 52. *Wesniphargus nichollsi* (Straškraba) male "b" 2.8 mm peraeopods 6 and 7 (part), male "d" 2.8 mm dactyls of gnathopods 1 and 2, female "a" 5.0 mm coxae 3–7.

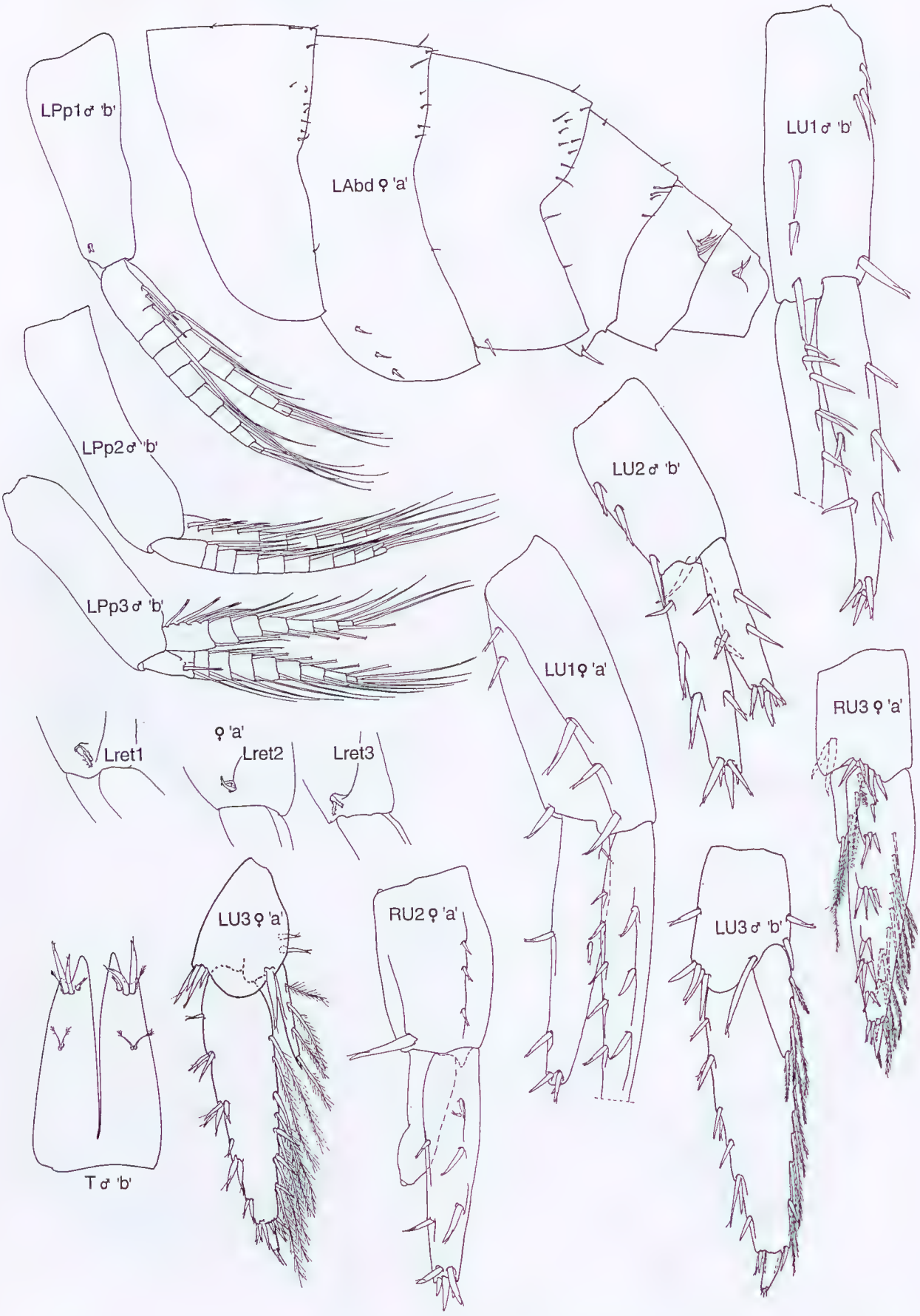

Fig. 53. *Wesniphargus nichollsi* (Straškraba) male "b" 2.8 mm pleopods, left uropods and telson; female "a" 5.0 mm abdomen, retinacula, uropods.

distolateral robust setae. *Pleopods* (Fig. 53): similar; peduncles naked except for a pair of retinaculae; rami moderately long of 8-7, 10-7, 9-7 lateral and medial articles respectively; basal article of the inner rami armed with several terminally bifid setae with asymmetrical apices, some with "diamond" heads, some symmetrical. *Uropods* (Fig. 53). Third uropod: extending beyond first and second in the intact specimen; uropod lengths relative to uropod 1 uropod 2 0.7, uropod 3 0.75. First uropod: peduncle length 1.1× outer ramus, 0.85× inner; outer margin with one apical robust seta and two dorsal robust setae, medial margin with three small basal robust setae and one apical robust seta; lateral ramus shorter than medial, both with two rows of marginal robust setae, the lateral apex with four robust setae, the medial with five. Second uropod: peduncle 0.8× length of the inner ramus with one apicodorsal robust seta and three medial robust setae; outer ramus shorter than the inner—70:100—both rami with two strong rows of marginal robust setae, apices with five robust setae. Third uropod: peduncle length 0.4× outer ramus, much longer than urosomite three—2.9×—with an apicolateral cluster of four faciosubdistal robust setae and a long dorsal robust seta, single mid-medial and mid-lateral robust setae; outer ramus proximal article with six lateral robust seta clusters of 1-2-2-1-2-1 robust setae, the medial margin with a row of seven setae and one distal robust seta; distal article small, 0.14× proximal, with three dorsal sub apical short setae; inner ramus length 0.3× outer, with three medial plumose setae and one apical plumose seta. *Telson* (Fig. 53): elongate, longer than urosomite three; cleft 85%; apices extended mediodistally as short lobes, subapices each with three robust setae in a transverse row, plus a single penicillate setule arising at the base of the largest, most lateral, robust seta; each lobe with a pair of penicillate setules dorsolaterally at M0.6.

Description of female "a". As for male "b" except in the following: *Body*: 5 mm. *First antenna* (Fig. 49): flagellum with seventeen articles, aesthetascs present on articles 4–17; accessory flagellum extending to M0.6 of third article of primary flagellum. *Second antenna*: flagellum without calceoli. *Gnathopods* (Fig. 51): coxal plate of second gnathopod with four long and three short apical setae; carpi longer than male—0.7 to 0.8× propodus; robust setae at corner of palm three (rather than four); posterior margin of propodus with an additional submarginal robust seta; dactyls with two recumbent robust setae on the inner margins *Peraeopods*: coxa 3 with three long and two short apical setae, no row of facial setae; coxa 4 emarginate with 12 short and two long ventral setae and two posterior setae on the anterior face; coxa 5 anterior lobe strongly reduced with one posterior seta on the anterior lobe and one posterior seta on the posterior lobe; coxa 6 with one posterior seta only, coxa 7 with two postventral setae and one posterior seta. *Oostegites* (Fig. 52): present on coxae 2–5; oostegites two to four broadly ovate with long, strong regularly spaced marginal setae; oostegite five more slender, otherwise similar. *Epimera* (Fig. 53): with sparse posterior setation, ventral face of epimeron two with three robust setae, of epimeron three with one robust seta. *Pleonites* (Fig. 53): 1–4 with small posterior robust setae, 5 and 6 bearing strong lateral spination. *Urosomite one* (Fig. 53): with strong articulate ventrodistal robust seta at the base of uropod 1. *Pleopods* (Fig. 53): each bearing pair of retinacula, without accessory retinacula or robust setae. *Uropods* (Fig. 53): rami of first uropod both with four apical robust setae; peduncle of third uropod with five (rather than four) apicolateral robust setae; outer ramus proximal article with 1-3-4-2-3-2 lateral robust setae, distal article with two sub terminal setae.

Description of male "d". *Body*: length 2.8 mm. *Gnathopods* (Fig. 52): subrectangular, similar size, less spinous than female "a". *Peraeopods* (Fig. 51): peraeopod 6 much longer than seven—1.3×—both with long basodactylar setae as long or longer than dactyl; peraeopods without other setae; article 2 of peraeopod 6 with moderate single posterior robust setae, anterior robust setae stronger, several paired; article 2 of peraeopod 7 with small to moderate posterior robust setae, few anterior robust setae, none paired; anterior robust setae of both peraeopods 6 and 7 dominant to posterior.

Distribution. Mammoth Cave, and near Margaret River, Western Australia, 34°03'S 115°01'E.

Paramelitidae Bousfield, 1977

***Pilbarus* n.gen.**

Etymology. Named for the type location.

Type species. *Pilbarus millsi* n.sp.

Diagnosis. Pleonites with moderate, mostly posterior transverse dorsal setation, rostrum obsolescent, lateral cephalic lobes moderately projecting, antennal sinus strong. Eyes absent. Antenna one elongate, longer than antenna two, ratio of lengths of peduncular articles about 3:2:1.5, accessory flagellum 4-articulate; second antenna peduncle longer than flagellum—85:74; flagellum of male bearing large calceoli. Mandibular palp of three articles, ratio of lengths about 2:3:2 to 2:4:3, articles 1 and 2 naked laterally, article 2 with distal oblique row of five strong rastellate setae, article 3 falcate, setae CDE. Labium with weak inner lobes. Maxillae without medial setae: first maxilla inner plate linear, apically tapered, with two plumose apical setae; outer plate with nine left, ten right denticulate apical robust setae; palps asymmetric, left palp with slender apical robust setae, right with 2-articulated elements but mostly broad robust setae fused to the article. Second maxilla inner plate without oblique setae, with two plumose mediodistal setae slightly submarginal, both plates with long curved apical setae. Maxillipedal palp with few lateral setae, with dense medial and medioventral setae, article 3 with a row of setae basal to the dactyl, but no comb row. Coxae 1–4 moderately elongate, coxa 3 with a few weak posterior setae, coxa 1 subquadrate, not expanded apically, coxa 4 moderately emarginate, coxae 5–7 posteriorly dominant, shorter than four. Gnathopods small, propodus of first gnathopod of male expanded, wider; carpus of the second relatively long, articles 3 and 4 of the first and four of the second with long posterior scythe robust seta, not lobate; propodus rectangular, palms weakly oblique, robust setae at the corner of the palm two and three, along the palm moderately crowded, without triggers. Posterior robust seta sets on article 6 of peraeopods 3 and 4 evenly spaced, legs 5–7 elongate, second article moderately to broadly expanded posteriorly and lobate, dactyls of peraeopods 3–7 without additional setules. Coxae 2–6 with sac like gills, thoracic segments without sternal gills. Basomedial setae of inner rami of pleopods bifid, branches simple; retinacula two each peduncle with one or two accessory robust setae. Pleonites with dorsal setae or robust setae. Epimera without postventral robust setae, with ventrofacial robust setae and sparse posterior setae. Rami of uropods 1 and 2 extending unequally; each with two rows of robust setae; uropod 1 without basofacial robust setae; uropod 3 extended beyond 1 and 2 in the intact specimen;

peduncle short, variramous; outer ramus 2-articulate, the second article short, the inner ramus reaching to M0.4 or less in the female, to M0.7 of outer ramus of male; poorly armed. Telson moderate length, about the same length as urosomite three, without dorsal setation, tumid, cleft more than 80%, with apical and dorsal spination.

Additional Description. Flagellum of first antenna lacking major arms. Upper lip apical marg evenly rounded. Mandibular accessory blades (rakers) with interraker plumose setae, additional penicillate setae beyond rakers riding onto base of molar; molar with pappose apical seta, palp article 3 shorter than 2, article 2 without sparse basoanterior setae with few facial apicoanterior setae. Maxilla two both plates with rows of long distal setae. Maxillipedal palp article 3 with ranks of thin setae on inner edge, and a row of three long setae facial, basal to the dactyl; dactyl with two accessory spinules basal to the nail; the apex weakly produced, pubescent; the outer plate with a row of setose robust setae distally, continuous with a row of teeth medially, the inner plate with three thick robust setae and plumose setae apically and a long medial row of plumose setae. Dactyl of gnathopods reaching ends of palms, some with small recumbent inner tooth like robust seta fused to dactyl, and several setules at inner nail articulation line, leg six longer than seven, legs 5–7 article 2 posterior setae small, regularly spaced. Sternal processes absent, epimera without postventral teeth. Pleopods similar, rami subequal. Apicolateral corner of peduncle of first uropod with one robust seta, rami of uropods 1 and 2 subequal, with four and five apical robust setae. Third uropod with or without facial robust setae, rami without plumose medial setae, ventrodistal robust seta on urosomite one at the base of uropod 1 long and strong, longer than *Austrocrangonyx*.

Relationship. This genus differs from other Paramelitidae, except *Antipodeus*, in the absence of sternal gills. Despite this it is closest to *Austrogammarus* in the form of the antennae, palp of first maxilla, gnathopods, and third uropod. *Pilbarus* differs from *Austrogammarus* in the absence of eyes, longer first article of the mandibular palp which lacks A setae but bears C setae, absence of medial setae on the first maxilla inner plate, absence of long straw like pubescence on the second maxilla, absence of dense lateral setae on the maxillipedal palp, presence of inner lobes on the labium, reduction of the palmar robust setae, more expanded and lobate second articles of peraeopods 5–7, absence of coxal gill 7 and of sternal gills, absence of marginal setation on the third uropod and of dorsal setation on the telson, and the presence of a long and strong robust seta on the first urosomite at the base of the first uropod. *Pilbarus* differs from *Austrocrangonyx* in absence of medial setae on the maxillae, reduced numbers of retinacula and presence of accessory retinacula, greater numbers of ventrofacial robust setae of the epimera, and presence of single rather than paired apicolateral robust setae on the peduncle of the first uropod. *Pilbarus* is similar to *Uroctena* in the absence of eyes, poor setosity of the mandibular palp, asymmetry of the palps of the first maxilla, weakly oblique gnathopodal palms, broad ovate expansion of the second article of peraeopods 5–7, form of the first and second uropods and length of the outer ramus of the third uropod, and absence of posteroventral epimeral teeth, but differs in that lateral cephalic lobes project moderately, accessory flagellum of the first antenna is no more than 4-articulate, second antenna is not pediform and calceoli are present on the male antenna, first article of mandibular palp relatively long, third article strongly rather than weakly falcate, with CDE setae only, labium bearing inner lobes, inner plate of first maxilla linear rather than ovatotriangular, outer plate with nine or ten (cf. 11) apical robust setae, medial setae of maxillipedal palp dense rather than moderate, apex of the third article pubescent, coxae 1–4 moderately long rather than short, coxa 1 not expanded apically, carpus of second gnathopod long, dactyls of peraeopods without additional spinules, thoracic segments without sternal gills, pleopods bearing spinous accessories to the retinacula, third uropod variramous being parviramous in the female and almost magniramous in the male, telson without dorsal setation but with additional dorsal spination. The genus is similar to *Hurleya* in the presence of only sparse lateral setae on the maxillipedal palp; coxal gill 6 is not reduced; but differs in many ways, including the ratio of lengths of peduncular articles of the first antenna; coxa 1 not short; gnathopods are not large, but are sexually dimorphic and bear scythe robust setae; palmar robust setae are reduced and simple; peraeopod 6 is longer than seven; articles 2 of peraeopods 5–7 are expanded and lobate; dactyls of the legs are not lobate; accessory retinaculae are present on the pleopods; third uropod is extended and variramous; telson is cleft 83% rather than 63% and has both apical and dorsal spination. *Pilbarus* is similar to *Antipodeus* in the fusion of strong palp setae of right the first maxilla; the small size of gnathopods; broad expansion and presence of postventral lobes of article 2 of peraeopods 5 and 7; broad oostegites; and differs in absence of eyes; greater number of accessory flagellum articles; presence of calceoli in the male; longer first article of the mandibular palp and poor setation of the second palp article, and lack of A setae; presence of inner lobes of the labium; absence of trigger robust setae on the gnathopodal palms; absence of coxal gill 7; uropod 3 variramous; telson with basofacial arms; and the ventrodistal robust seta on urosomite one long and strong. The new genus is similar to *Chillagoe* in the asymmetry of the palps of the first maxilla; the absence of a gill on coxa 7 and lack of reduction of gill 6; but differs in that lateral cephalic lobes do not project strongly; flagellum of antenna two is not shorter than peduncle; first article of mandibular palp is relatively short article 2 poorly setose, and C setae present; inner lobes present on labium; coxa 4 moderately emarginate; palms not strongly oblique; palmar robust setae reduced; oostegites are not slender; third uropod has an inner ramus; telson cleft more than 70% and with four rather than one apical robust seta. *Pilbarus* is similar to *Toulrabia* in the terminal setae of the mandibular palp are CDE; palps of first maxilla are similarly asymmetric; palmar robust setae of gnathopods are simple; coxae 2–6 bear gills, the sixth not reduced; peduncles of pleopods bear two retinacula and accessory spinules; but differs in the third peduncular article of antenna one is relatively long; flagellum of the second antenna not

greatly shorter than peduncle; second articles of peraeopods 5–7 ovate rather than pyriform; dactyls of peraeopods not multi-spinose; coxae 2–4, rather than 2–5, bear oostegites; uropod 3 is moderately extended rather than poorly, am d the outer ramus has two rather than one article; the telson is longer than broad, cleft 83% rather than 60%, without setae, but with basolateral spination. *Pilbarus* is similar to *Protocrangonyx* in that eyes are absent; the flagellum of antenna two is not much shorter than peduncle; palps of the first maxillae are asymmetric; coxae 2–6 bear gills; and differs in that the body is not sub vermiform; the accessory flagellum of antenna 1 is 4- rather than 2-articulate; ; calceoli occur on the second antenna; third article of mandibular palp is falcate, and C setae are present; the labium has inner lobes; coxae are moderately long, not short, and coxa 4 emarginate; gnathopodal palms are slightly not strongly oblique; palmar corner robust setae are reduced and palmar robust setae without triggers; leg seven is shorter than six and articles 2 of peraeopods 5–7 ovate and moderately lobate; uropod 3 is strong, not feeble, is extended, variramous, and the outer ramus 2-articulate; telson cleft, moderately long, and with dorsolateral as well as apical spination; peduncles of pleopods weakly to moderately setose, the outer rather than inner rami shortened; ventrodistal robust seta at the base of uropod 1 present and strong and long.

Pilbarus millsi n.sp.

Figs 54–57

Etymology. Named for the type locality.

Type locality. Deep Reach Pool, Pilbara Springs, Millstream, northern Western Australia, on the Fortescue River, 21°37'S 117°06E.

Material Examined. HOLOTYPE (Australian Museum P51378) female "a", 9 mm. ALLOTYPE (Australian Museum P51379) male "b", 7 mm. Others in the type series: females "c" 7 mm and "d" 6 mm, several small juveniles 3–5 mm. Collected by W. Ponder and W. Edgecomb, Deep Reach Pool, Pilbara Springs, Millstream, Western Australia, September, 1987. Australian Museum Collection P38475.

Diagnosis. With the characteristics of the genus

Description of holotype (female "a"). *Body* (Fig. 54): pereon with sparse setation; pleon with strong transverse posterodorsal setation and spination, length 9 mm. *Head*: small anterior marginal setae at the base of antenna one; rostrum weak; lateral cephalic lobe moderate; antennal sinus moderate; eyes absent. *First antenna* (Fig. 54): length 0.6× body, 1.9× second antenna; peduncle sparsely setulate, ratio of lengths of articles 10:7:5; flagellum much longer than peduncle, ratio of lengths 200:82, setae sparse, flagellum of 33 articles; accessory flagellum 4-articulate, reaching to the end of article 4 of the primary flagellum, without aesthetascs or calceoli. *Second antenna* (Fig. 54): length 0.3× body; peduncle longer than flagellum, ratio of lengths 85:74; article 4 longer than five—33:29—articles 3–5 moderately setose; flagellum of fourteen articles, moderately setose, without aesthetascs or calceoli. *Left mandible* (Fig. 55): palp of three articles, ratio of lengths 8:16:11, article 1 naked, article 2 naked medially and laterally, mediodistal face bearing an oblique row of six strong rastellate setae the longest reaching beyond M0.5 of the third article; third article broad, falcate, facially pubescent, setae 1C13D4E; incisor six toothed; lacinia mobilis five toothed; accessory blades of three rakers and three plumose setae, with three blunt bent brushy setae and fine setules onto the base of the molar; molar triturative with an anterior plumose seta and short posterior pappose seta. *Right mandible* (Fig. 55): palp articles 1 and 2 naked laterally and medially, second article with an oblique distal row of five strong rastellate setae reaching to beyond M0.5 of the third article, third article with long basofacial setules, facial pubescence, setae 14D4E; incisor with seven teeth; lacinia mobilis bifid, denticulate the posterior lobe bearing anterior and posterior teeth; accessory blades of two rakers and two plumose setae; molar triturative with short anterior plumose seta and long posterior pappose seta. *Left first maxilla* (Fig. 55): palp article 2 with seven simple slender distal robust setae; outer plate with nine apical denticulate robust setae; inner plate with two apical plumose setae, the medial slightly sub apical. *Right first maxilla* (Fig. 55): with five broad mediodistal to apical robust setae fused to the article and a single strong articulated lateral sub apical robust seta and one plumose seta; outer plate with ten apical denticulate robust setae; inner plate with two apical plumose setae, the medial seta slightly sub apical. *Second maxilla* (Fig. 55): lateral margin of outer plate without additional seta, inner margin of inner plate with two plumose setae subdistal sub marginal to the medial edge. *Maxilliped* (Fig. 55): outer plate with long medial robust setae and setae, moderately oblique; from the mid-medial margin ten strong robust setae, which increase in size distally, form a moderately oblique row across the face of the article, the ultimate robust seta mid apical, forming a continuous row with five apicolateral plumose setae; facial to the robust seta row lie four ranks of 1-1-2-2 slender setae; inner plate with five plumose medial setae, transverse row of three stout naked tooth like robust setae, three apicolateral and one ventrofacial plumose seta, and one mid apical fine seta. *First gnathopod* (Fig. 56): coxal plate with moderate apical and apicoanterior marginal setae; articles 3 and 4 bearing strong posterior scythe robust setae, rastellate on article 4; carpus short, about 0.55× propodus, slightly lobate, bearing many strong posterior rastellate robust setae; propodus long, trapezoidal, the posterior margin bearing ranks of moderate rastellate robust setae, corner of palm with one strong and two long slender lateral robust setae and one naked medial robust seta; palm slightly oblique with few short simple robust setae; dactyl with a transverse rank of four accessory setules at M0.4, nail reaching the end of the palm. *Second gnathopod* (Fig. 56): slightly larger than first gnathopod; coxal plate with two posterior setae, bearing sac like gill and broad sparsely setose oostegite; article 4 bearing long posterior robust setae; carpus elongate, as long as the propodus, bearing posterior ranks of many long simple setae; propodus elongate; posterior ranks of many long simple robust setae similar to but slightly shorter than of the carpus; palmar corner with one blunt medial robust seta and two lateral bifid robust setae, palm convex, robust setae simple, moderately long and crowded; dactyl with blunt recumbent inner tooth like robust seta, four facial spinules, nail reaching to the palmar corner. *Peraeopods* (Fig. 56): coxa 3 with few apical setae, posterior corner indistinct, posterior margin with one or two setae; coxa 4 sparsely setose apically with a row of posterior setae, moderately emarginate; both coxae bearing sac like gill and apically setose oostegite; peraeopods 3 and 4 similar, longer

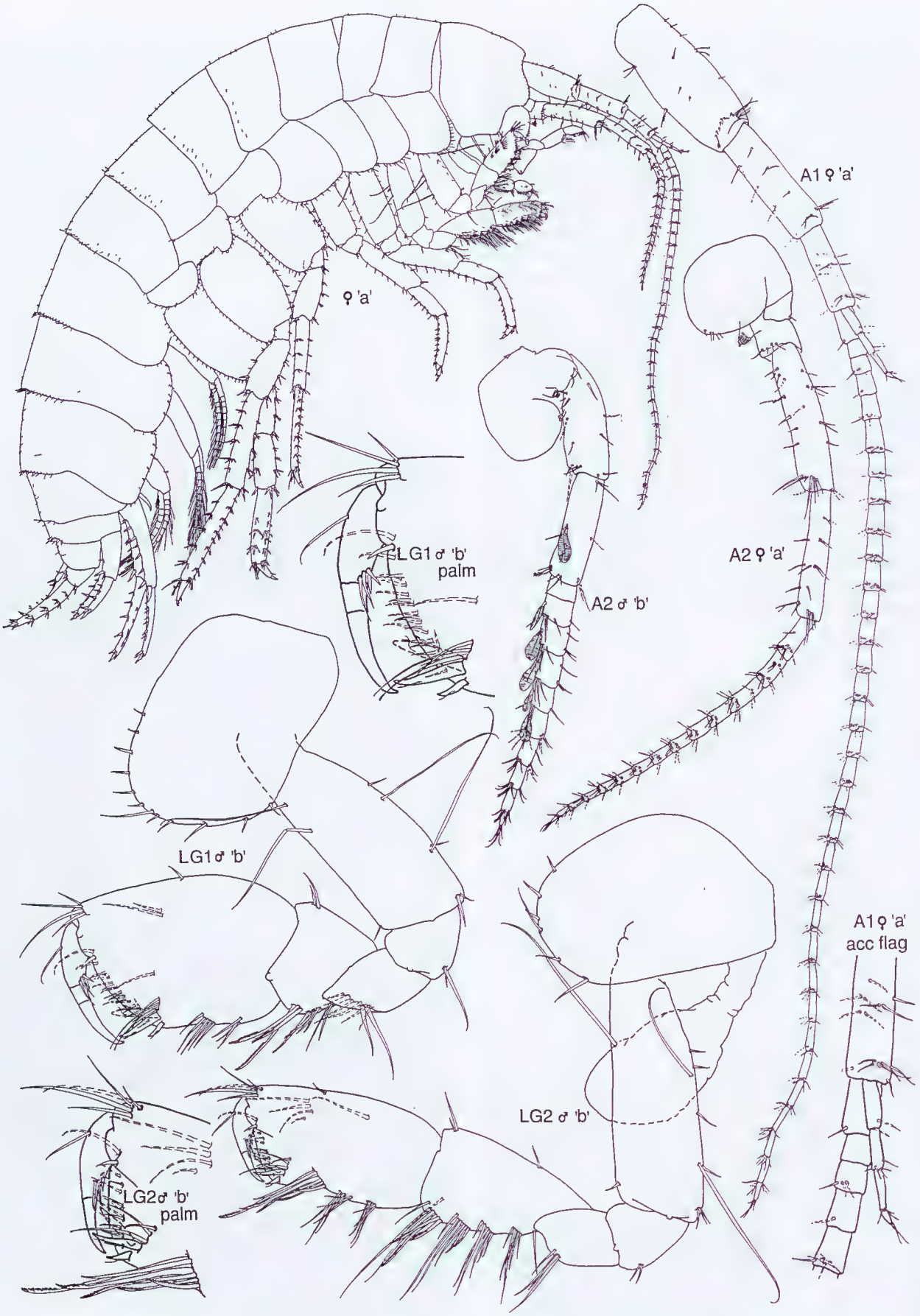

Fig. 54. *Pilbarus millsi* n.sp. holotype female "a" 9 mm whole specimen, antennae, accessory flagellum; allotype male "b" 7 mm antenna two, gnathopods 1 and 2.

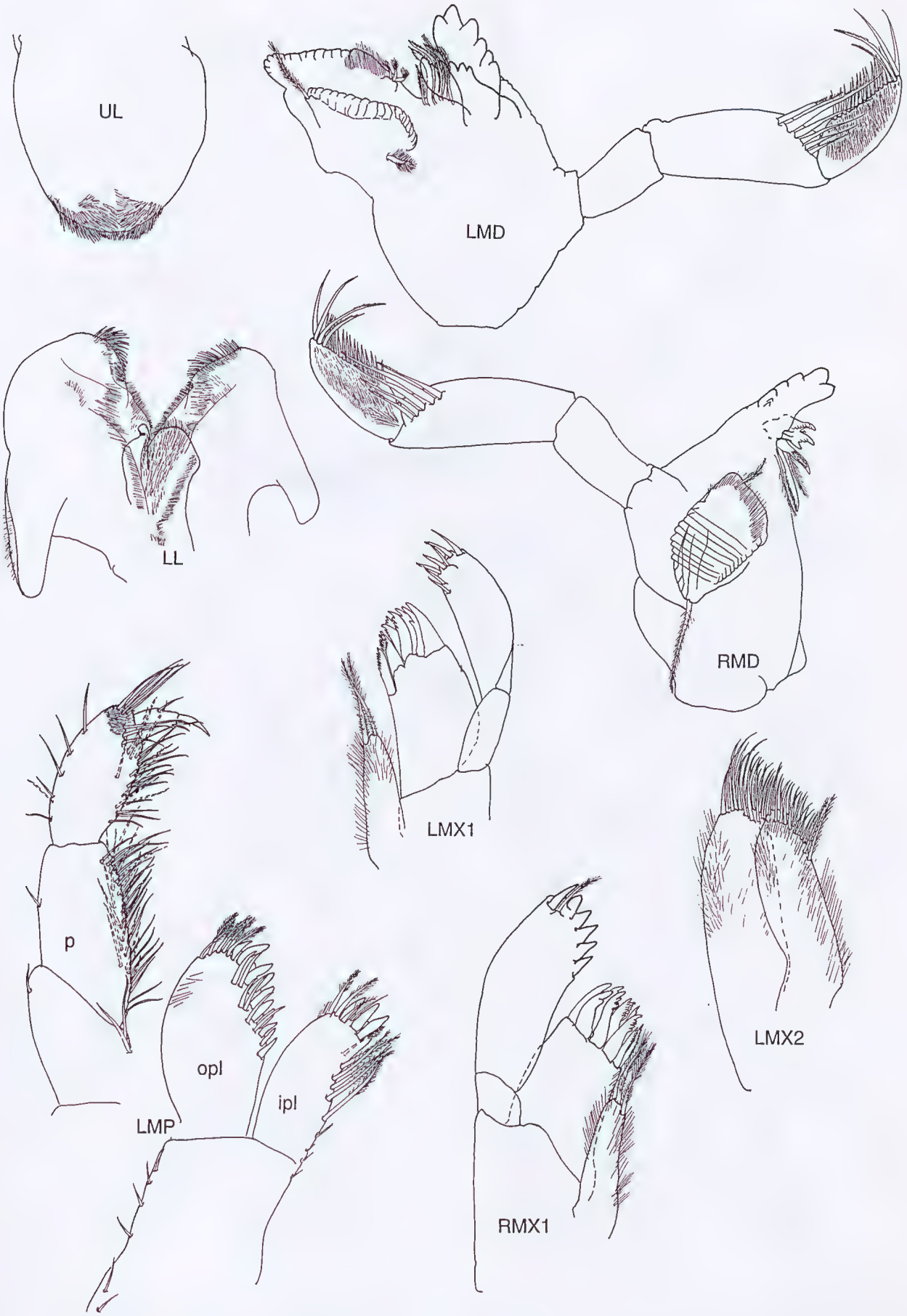

Fig. 55. *Pilbarus millsi* n.sp. holotype female "a" 9 mm; mouthparts.

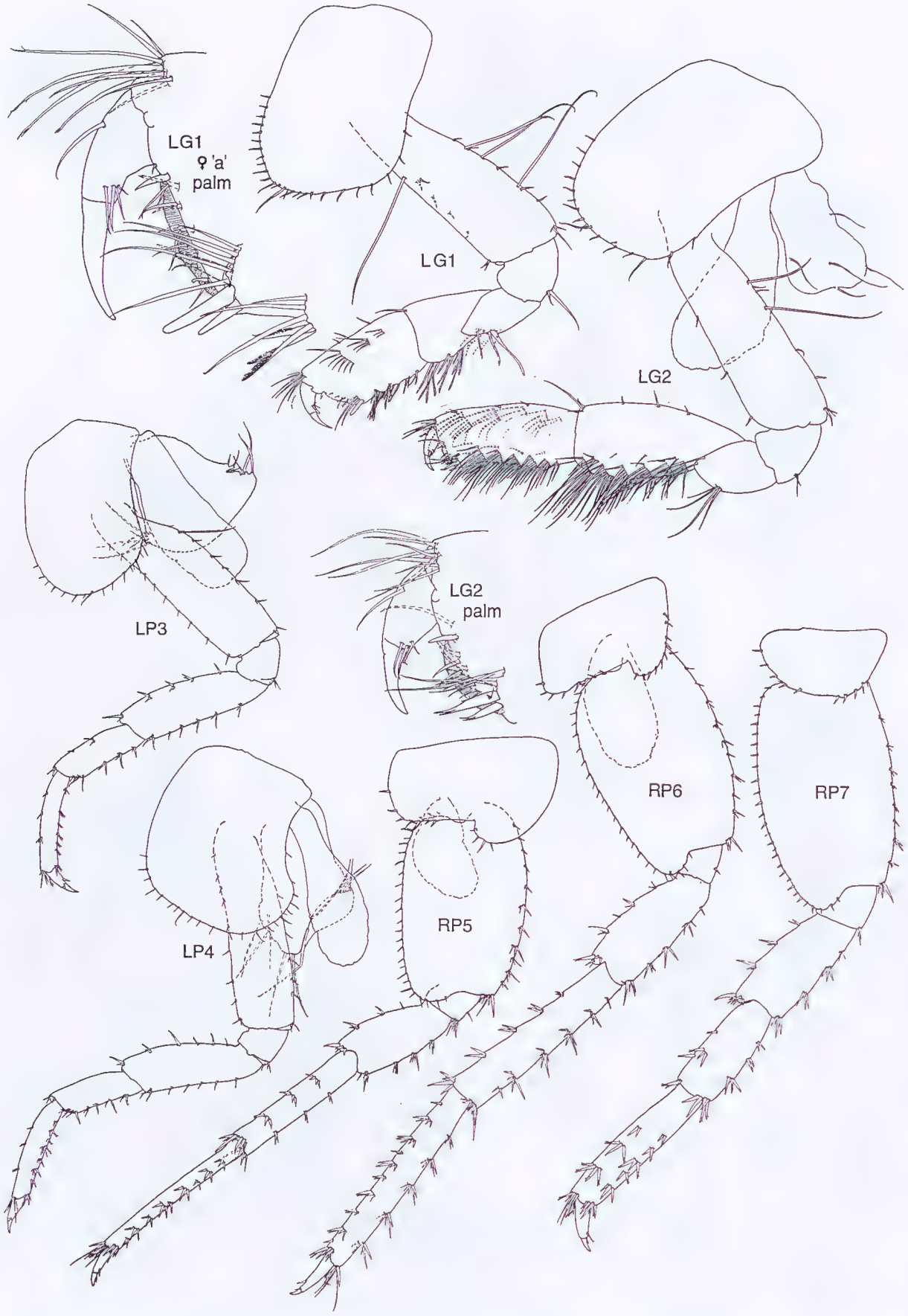

Fig. 56. *Pilbarus millsi* n.sp. holotype female "a" 9 mm; legs (all drawings except those indicated); female "c" palm of first gnathopod.

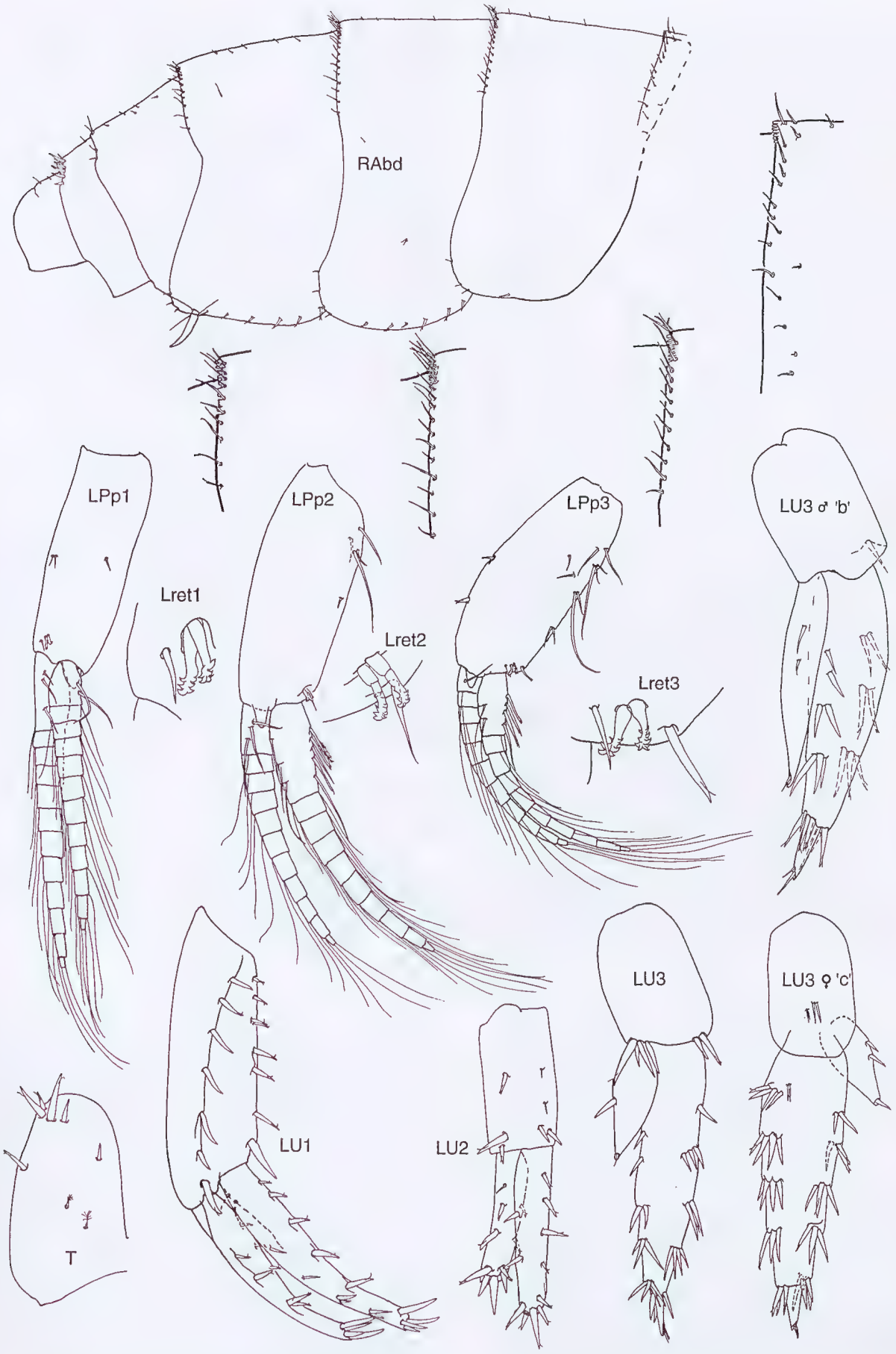

Fig. 57. *Pilbarus millsi* n.sp. holotype female "a" 9 mm; abdomen, gills, pleopods, uropods, telson (all drawings except those indicated); allotype male "b" 7 mm, third uropod; female "c" 7 mm, third uropod.

than gnathopod two, articles 4 and 5 moderately setose posteriorly, article 6 of peraeopod 4 with more posterior robust setae than peraeopod 3: peraeopods 5–7 similar, six longest, seven shortest, coxae shorter than coxa 4, posterior lobe dominant, coxae 5 and 6 bearing sac like gills, articles 2 expanded posteriorly, ovate, moderately lobate postventrally, with many short posteromarginal robust setae, other articles moderately equipped with short stout anterior and posterior robust setae; dactyls of peraeopods 3–7 each with one distofacial and one mediomarginal setule. *Epimera* (Fig. 57): without postventral teeth, posterior angles rounded, posterior setae sparse, with 1-6-6 ventrofacial robust setae. *Pleon* (Fig. 57): with sparse dorsal setae; posterior margins of pleonites 1–3 with dense, short transverse setules, and small dorsolateral truncated robust setae; pleonite 4 with sparse, weak posterior spinules; pleonite 5 with a submarginal transverse rank of five moderate and three small robust setae. *Urosomite one* (Fig. 57): with a long strong robust seta at the base of the first uropod. *Pleopods* (Fig. 57): peduncles with scarce armature, peduncle one with two mid facial spinules, two retinacula and one accessory robust seta; peduncle two with four mediobasal and one mid medial robust seta, two retinacula and one accessory robust seta; peduncle three with several strong and weak medial robust setae, two short lateral robust setae, two retinacula and two accessory robust setae; rami similar, basomedial setae of inner rami bifid; rami with 12-12, 11-10, 11-10 articles respectively. *Uropods* (Fig. 57). First uropod: peduncle length 1.2× outer ramus, 1.0× inner ramus; outer margin with dorsal row of six moderate robust setae and one distolateral robust seta; inner margin with seven dorsal and one distomedial robust seta; both rami with two rows of dorsal robust setae and four apical robust setae. Second uropod: peduncle as long as outer ramus, 0.8× inner ramus, weakly spinous on both margins, with paired distolateral and distomedial robust setae; rami with two rows of dorsal robust setae, each with four apical robust setae. Third uropod: variramous; peduncle length 0.5× inner ramus, 1.2× outer ramus; without marginal or facial arms; pair of distolateral robust setae and rank of four distomedial robust setae basal to the inner ramus; proximal article outer ramus with four transverse lateral ranks of 1-3-3-4 and one distal robust seta, and five transverse medial ranks of 1-1-2-3-4 and one distal robust seta; distal article small with three fine apical setules; inner ramus short, with one mid medial robust seta and one apical setule. *Telson* (Fig. 57): slightly shorter than urosomite three; lobes cleft 83%, laterally tumid; lateral sub apical transverse row of two large and two small robust setae, marginal dorsolateral robust seta at M0.6, small submarginal dorsomedial robust seta at M0.67 and mid dorsal penicillate setules at M0.3 and M0.4.

Description of allotype male "b". As for female "a" except in the following. *Body*: length 7 mm. *Second antenna* (Fig. 54): peduncle articles 4 and 5 with sparse arms, article 5 bearing large calceolis ventrally at M0.0.5; flagellum of ten articles with moderate setation; articles 2–6 bearing large ventral calceoli. *Mandibles*: left palp article 3 with setae 8D4E; right palp with setae 1C8D5E. *First gnathopod* (Fig. 54): articles 3 and 4 with strong simple posterior robust setae; carpus short, with moderate and long rastellate setae; propodus ovate rather than long, length 1.2× width; posterior margin with two transverse ranks of moderate setae, palmar corner rounded, with one large medial tooth like-robust seta, two lateral robust setae; palm slightly convex with moderately crowded simple robust setae; dactylus with a mid rank of four accessory spinules, nail reaching to the palmar corner. *Second gnathopod* (Fig. 54): coxal plate with sparse, moderately long apical setae, without posterior setae, bearing a large sac like gill; article 4 with several long, simple robust setae; carpus moderately long, 0.7× propodus, with four transverse ranks of mixed simple and rastellate robust setae; propodus trapezoidal, longer than wide length 2× width, posterior margin with two ranks of moderate simple robust setae and one of mixed long simple and rastellate robust setae; palmar corner broadly curved, with one medial and two lateral strong robust setae; palm convex, with moderate numbers of short simple robust setae; dactyl with four accessory setules, nail reaching to palmar corner. *Third uropod* (Fig. 57): variramous, outer ramus 1.45× inner ramus, 0.45× peduncle; peduncle without marginal or facial arms, with a single moderate distolateral robust seta adjacent the base of the outer ramus; outer ramus proximal article with lateral transverse ranks of 2-2-3 marginal robust setae and three distal robust seta, medial transverse ranks of 1-1-2-3 marginal robust seta and four distal robust setae; distal article small, naked except for two small apical setae; inner ramus with two mid facial setae and one small distal seta.

Description of female "c". As for female "a" except in the following. *Body*: length 7 mm. *Mandibles*: left palp article 3 with setae 1C12D4E; right palp setae 1C11D4E. *First gnathopod* (Fig. 56): palmar corner with one medial strong naked robust seta and five long slender and two strong naked lateral robust setae; palm moderately convex slightly oblique, with moderate numbers of simple robust setae. *Third uropod* (Fig. 57): variramous, peduncle length 0.5× outer ramus, 1.5× inner, with three small facial setae; outer ramus 2-articulate, proximal article with lateral transverse ranks of 4-4-4-3 and three distal robust setae, two small facial setae adjacent the most basal rank of robust setae, and medial transverse ranks of 2-3-3-3 and 4 distal short robust setae; distal article short with two small apical setules; inner ramus with two mediofacial short robust setae and one short distal robust seta.

Description of female "d". *Body*: length 6 mm. *Right mandible*: right mandibular palp article 3 setae 1C9D5E. Otherwise similar to female "a".

Distribution. Deep Reach Pool, Pilbara Springs, Millstream, Western Australia, 21°37'S 117°06E.

Synopsis

Thirty described species of Australian stygobiont amphipods were listed by Bradbury & Williams (1997). The present paper significantly extends this number by adding a further fourteen species and noting another species (*Wesniphargus nichollsi*) previously described, now regarded as a troglophile. Two of the new species fall within the two families which previously contained most of the diversity (Melitidae and Paramelitidae), but most are unequivocally neoniphargids and hence now bring this family into more or less equal position as a contributor to diversity of Australian stygobiont amphipods. Table I provides an updated synopsis of known forms arranged in the same way as did Bradbury & Williams (1997, table I). Figure 58 similarly documents the geographical distribution of all described forms (with some exceptions, as noted).

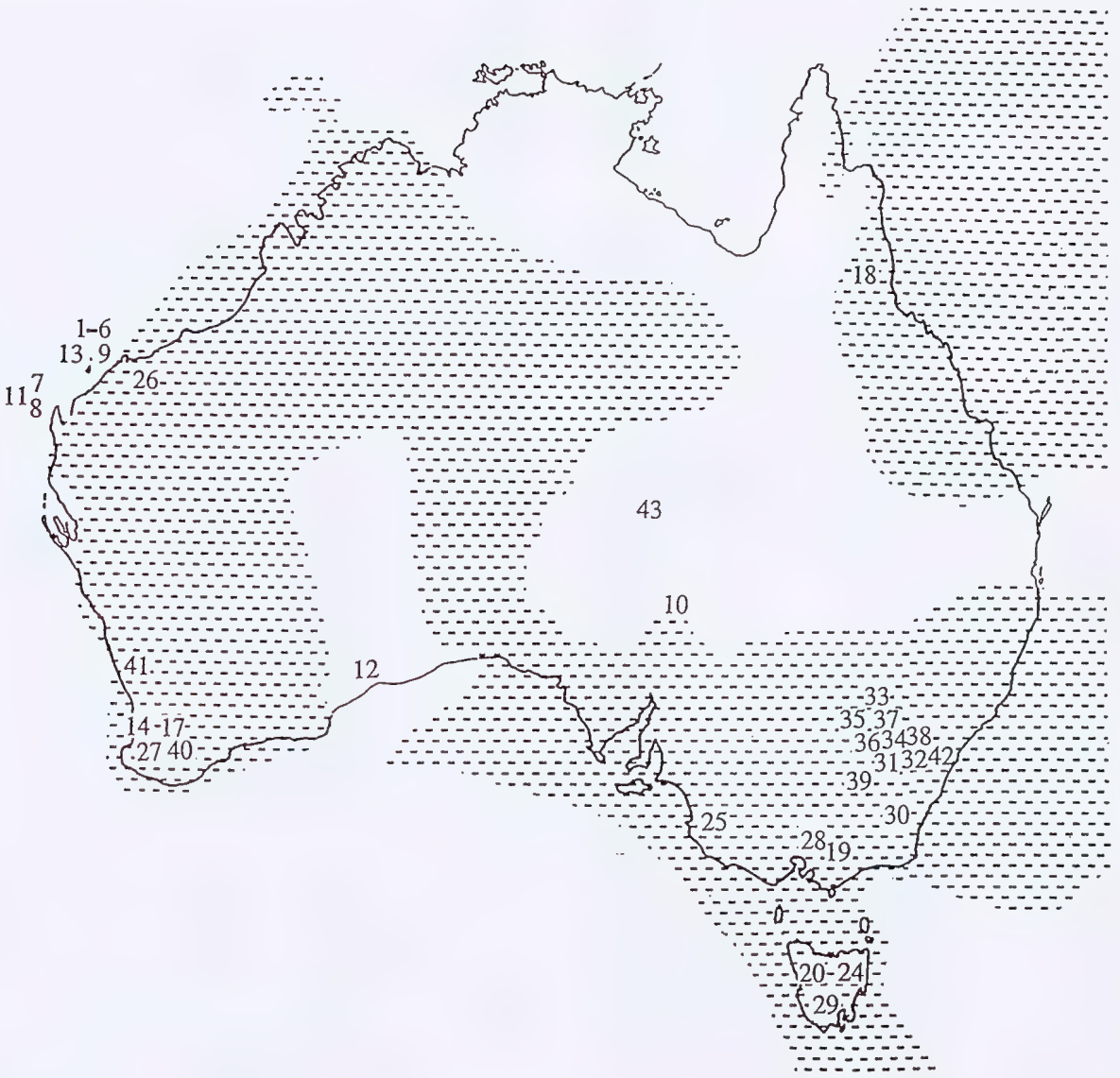

Fig. 58. Distribution of known stygobiont Australian amphipods. Stippled area indicates landmass not inundated during the Cretaceous (119–114 million years ago). Numbers indicate species shown in Table 1—*Austrochiltonia australis* (44) widespread and *Pseudomoera fontana* (45) known from widely separated locations in the southeast, not shown.

Discussion

The taxonomic and distributional information given in this paper support the general conclusions of Bradbury & Williams (1997) on the extent, nature and causes of stygobiont amphipod diversity in Australia. Thus, the description of fourteen new species confirms the significant diversity of this fauna in Australia in both hadzioid and crangonyctoid families, and the geographical distribution of these new species falls clearly within areas of Cretaceous marine transgression (melitoid species) or areas not so inundated during the Cretaceous (Paramelitid and Neoniphargid species). As further confirmation of the importance of karst in promoting stygobiont diversity, note that the new crangonyctoid species (except *Wesniphargus yanchepensis*) were collected from caves in the karst systems of New South Wales.

Much remains for investigation with regard to the stygobiont amphipods of Australia, not least in respect of their evolution and the adaptive and selective processes involved in this. Many areas of karst (for example, eastern Victoria, southeast South Australia, Nullarbor Plain, Camooweal caves in western Queensland, and many caves in Tasmania), as well as other caves (for example, the lava tubes at Undara in Queensland) have yet to be thoroughly examined, or their fauna described. Several of these sites are known to contain populations of stygobiont amphipods (Eberhard *et al.*, 1991; Eberhard & Spate, 1995), and will be the subject of future reports. Australia must now be recognised as a major centre of stygobiont amphipod diversity and we hope the present paper will both promote and support further investigations which build on this recognition.

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Table 1. Systematic position and geographic distribution of Australian subterranean amphipods. Modified after Bradbury & Williams (1997). NP: National Park; NSW: New South Wales; SA: South Australia; WA: Western Australia.

TAXON	DISTRIBUTION	HABIT	NO.
Melitidae			
Nedsia straskraba Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	01
N. fragilis Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	02
N. humphreysi Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	03
N. hurlberti Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	04
N. macrosculptilis Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	05
N. sculptilis Bradbury & Williams, 1996a	Barrow Island, WA	troglobite	06
N. douglasi Barnard & Williams, 1995	North West Cape, WA	troglobite	07
Liagoceradocus branchialis Bradbury & Williams, 1996b	North West Cape, WA	anchialine troglobite	08
L. subthalassicus Bradbury & Williams, 1996b	Barrow Island, WA	anchialine troglobite	09
Brachina invasa Barnard & Williams, 1995	Flinders Ranges, SA	hyporheic interstitial	10
Norcapensis mandibulis n.sp.	North West Cape, WA	troglobite	11
Melita like.	Nullarbor Plain, WA	troglobite	12
Bogidiellidae			
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A New Genus and Two New Species of Cypridinidae (Crustacea: Ostracoda: Myodocopina) from Australia

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ABSTRACT. A new genus and two new species of Cypridinidae, *Lowrya taiti* and *Lowrya kornickeri*, are described from New South Wales, Australia. Both species are scavengers. They possess an elongate frontal knob and a structurally coloured red area on the rostrum of the carapace. The adult males of these species bear large compound eyes with very large dorsal ommatidia and very large "suckers" arising from cup-shaped processes near the base of the c-setae of the first antennae. *Lowrya taiti* possesses "coelotrichs", which are unusual evagination/setal sensillae of the carapace (Parker, submitted), and a concave anterior margin of the left rostrum only. *Lowrya kornickeri* is unusual because it bears an additional small "sucker" distal to the large basal "sucker" on the basal setule of the b-seta of the male first antenna.

PARKER, A.R., 1998. A new genus and two new species of Cypridinidae (Crustacea: Ostracoda: Myodocopina) from Australia. Records of the Australian Museum 50(1): 1–17.

Cohen (1982) reported 24 genera and about 100 species worldwide in the Cypridinidae. Since 1982 about 60 additional species of cypridinids have been described. Only a few species of cypridinids have previously been reported as scavengers (Sars, 1922; Natas, 1979; Collins *et al.*, 1984; Stepien & Brusca, 1985; Cohen, 1983; Vannier & Abe, 1993).

The Australian Museum has conducted extensive trapping of scavenging crustaceans in eastern Australian seas from 1986 to 1995 known as the SEAS (Scavengers of Eastern Australian Seas) Project. Scavenging cypridinids were present at all depths, and down to about 100 m depth they numerically dominate the scavenging guild, with numbers of individuals reaching to 75,000 per trap (J.K. Lowry, personal communication). From this collection an undescribed genus emerged, identified from other genera under a dissecting microscope by the possession of a red structural colour on the rostrum of the carapace. The two species described herein, *Lowrya taiti* and *L. kornickeri*, are from this new genus, caught during the above trapping program using single chamber traps designed by Keable (1995).

Lowrya taiti is distinguished from *L. kornickeri* by the presence of coelotrichs (concave sensilla; Parker, in prep.) forming a row on the external carapace surface parallel with the anterior, ventral and posterior carapace margins. *Lowrya taiti* also uniquely exhibits a concave margin of the left carapace rostrum only, with strong sclerotization in the corresponding supplementary region of the right carapace rostrum. *Lowrya kornickeri* is characterized by the presence of a small "sucker" distal to the larger, usual "sucker" of the basal setule of the b-seta of the male first antenna.

Skogsberg (1920) considered the "suckers" (although possibly olfactory organs; Kornicker, 1983) of the adult male first antennae, and the endopodite of the adult male second antenna, to be "the most noteworthy" in classifying the Cypridinidae. Kornicker (1983) illustrated the different types of "sucker" arrangements on the first antennae of adult male cypridinids, and their use in grouping genera. The exceptionally large size of the basal "suckers", and their extrusion from a separate cup-like basal section, of the c-setae on the adult male first antennae, are characters unique to *Lowrya* and *Sheina*.

Descriptions have been generated from the taxonomic data base program DELTA (Dallwitz *et al.*, 1993).

New definitions of types of hair-like structures for Myodocopina are used to standardize the terminology of homologous parts both within a specimen and within Crustacea, adapted from Watling (1989) (Fig. 1). A seta is a hair-like structure (extension of the cuticle) with an articulate base; a spine is a hair-like structure with a non-articulate base. Exceptionally broad setae and spines are given the prefix "robust". A setule is a "seta" which occurs on a seta or spine; a spinule is a "spine" which occurs on a seta or spine. Denticle refers to a broad (robust) spinule. Setous refers to a dense collection of setae, except when the setae are very fine and long which is referred to as hirsute; spinous refers to a dense collection of spines. Claws refer to the large robust setae or spines historically termed as such for Myodocopa, occurring only on the furca and the terminal article of the mandibular endopodite. Claw-like refers to the curved, robust nature of setae or spines bearing few broad denticles, giving the appearance of a "claw".

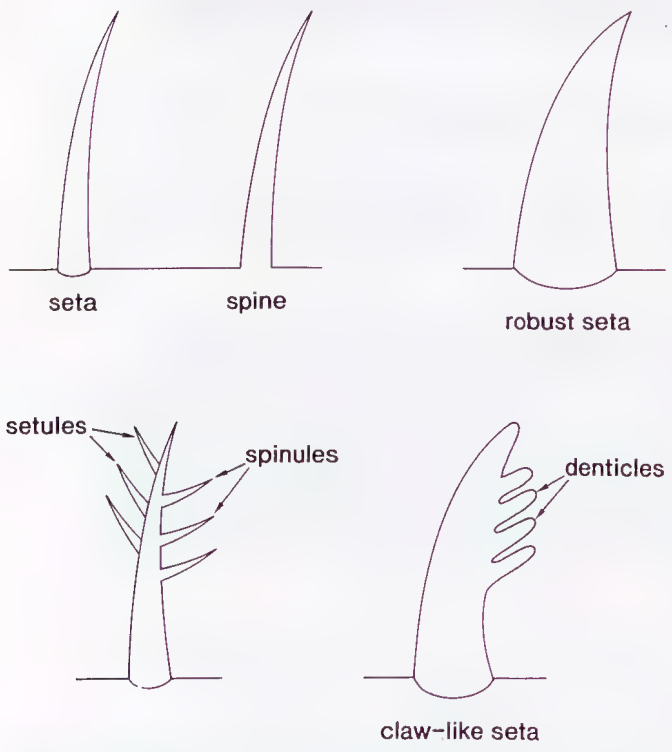

Fig. 1. Definitions of hair-like structures used in the following species descriptions.

Material is lodged in the Australian Museum, Sydney (AM), the National Museum of Natural History, Washington D.C. (NMNH) and the Natural History Museum, London (BMNH).

Systematics

Myodocopina

Cypridinidae

Lowrya n.gen.

Diagnosis. Unique characters are an elongate frontal knob and a spine mid-way along ventral margin of second exopodial article of the second antenna. Unusual characters are as follows. A rectangular oval carapace (with rounded corners); red colouration on rostrum when viewed from certain directions due to strong sclerotization (structural colour, not to be confused with maroon pigmentation of first antennae which is often visible through the carapace); lateral processes arising from rostrum, along dorsal edge of incisure. First antenna: very large basal "sucker" of c-seta on adult male first antennae, arising from separate cup-like basal section; some halophores (setules on first antennae; Parker, 1995, 1998) with spinules. Second antenna: endopodite with 3 articles; spine on ventral margin of second exopodial article; third exopodial article seta with proximal robust setae. Mandible with three broad terminal claws (of similar length), ventromedial and ventrolateral mandibular claws with very long spinules. Fourth limb: 1 α-seta (with many setules) and 2 β-setae. Sixth limb: terminal article short and approximately square. Seventh limb: few non-terminal and terminal setae; few terminal long and short teeth. Male copulatory "limb": hood with peak with an abrupt joint near inner edge of limb. Furca: very broad fourth claw; claws 2 and 4 fused to lamella. Upper lip: single unpaired anteroventral field of nozzles; short tusks. Posterior of male body: without dorsal folds.

Type species. *Lowrya taiti* n.sp.

Species composition. *Lowrya* contains *L. taiti* n.sp. and *L. kornickeri* n.sp.

Etymology. In honour of James K. Lowry, carcinologist, who discovered new guilds of scavenging crustaceans off Australia with unexpected compositions, including high proportions of cypridinids.

Remarks. *Lowrya* is most similar to the monotypic genus *Sheina* Harding, 1966. Both genera bear very large "suckers" on the c-setae of the male first antennae, which appear to be morphologically similar (arising from a basal cup-like process). These two genera are only known from

eastern Australia. *Lowrya* differs from *Sheina* in the shapes of its carapace and furca, and in that it bears a well-developed coxal endite on its mandibles, the c-seta (lateral seta) of the terminal endopodial article of the mandible lacks a dorsal hirsute pad (see Kornicker, 1986). *Lowrya* also shares some characters with *Vargula* Skogsberg, 1920, e.g., an upper lip with tusks without lobes, endopodite of second antenna with three articles (the second article with a seta). It can be noted that *Vargula subantarctica* Kornicker, 1975, for example, also bears some halophores with spines, and males of *V. psydrax* Kornicker, 1994, bear a first antenna with an almost cup-like process at the base of the c-seta, although the "sucker", which is not as well developed as in *Lowrya*, does not arise from this process. However, *Vargula* is polyphyletic and requires reorganisation (Cohen & Morin, 1990). *Lowrya* bears only one α-seta on its fourth limb, a character shared with *V. magna* Kornicker, 1984, *V. tsujii*, Kornicker & Baker, 1977, and *Kornickeria* Cohen & Morin, 1993, although *Lowrya* has a have very different carapace shape to these taxa. The sclerotization of the rostrum, forming lateral processes, in *Lowrya* is most similar to that of *Paracypridina* Poulsen, 1962, and to some extent *Heterodesmus* Brady, 1866, although *Lowrya* is separated from these genera by the possession of an endopodite of the second antenna with three articles.

Lowrya taiti n.sp.

Figs 1–4

Type locality. Off Providential Head, Bate Bay, NSW, Australia (34°07'S 151°10'E); baited trap set overnight at 46 m depth. Collected by J.K. Lowry, S.J. Keable and A.R. Parker on M.V. Krista, 14–15 January 1991. Total of 70 *Lowrya* sp. caught in trap (62 males), in addition to 11 other species of cypridinid ostracods, 3 species of cirolanid isopods, 3 species of lysianassoid amphipods, and 1 species each of a nebaliacean, gastropod and a polychaete. Undescribed species of the cypridinid ostracods *Paradoloria* (926 individuals), *Vargula* (860) and *Cypridinodes* (464) constituted the dominant scavenging species.

Type material. HOLOTYPE: AM P44618, adult female. PARATYPES: AM P44619, adult male; AM P45529, adult female; AM P45530, adult male; AM P45531, 3 adult males (undissected); BMNH 1995:1601–1602, 2 adult males (undissected); NMNH, 2 adult males (undissected).

Other material examined. AM P45532, adult male, cleaned using ultrasound, critical point dried, mounted on a scanning electron microscope (SEM) stub, and coated with gold (examined in a SEM).

Description of adult female characters.

COLOUR OF LIVING OSTRACODS. Beige with a red area above the incisure visible from certain orientations.

CARAPACE. Holotype: length = 1.27 mm, height = 0.81 mm; length/height = 1.57. Paratype: length = 1.36 mm, height = 0.91 mm; length/height = 1.49.

Shape: rectangular oval, very slightly protruding keel; margins straight for much of length dorsally, slightly rounded ventrally (Fig. 2E). Keel joined by slight dorsal concave curve to curved posterior margin of valve (Fig. 2D); dorsal edge of keel at about midheight of valve; dorsal edge of incisure slightly overlapping ventral edge at inner end, line on outer surface of valve curving from inner dorsal edge of incisure to anterior margin of valve (ventral to incisure) is faint. Tip of rostrum rounded; with smooth adjacent margins (Fig. 2A).

Valve surface smooth at low magnification, but with scale-like pattern visible on anterior margins with a light microscope at 100 times magnification (as in Fig. 5C); setae on valve surface medium sized and scattered evenly; 9 *muscle scars*, forming a triangle with smaller scars inside triangle (Fig. 2F).

Infold: infold posterior to rostrum with row of 11 setae, double type, parallel to valve margin, 9 of these setae are dorsal to incisure; 1 seta posterior to carapace infold row, double type; 4 setae anterior to carapace infold row, double type. Posterodorsal edge of incisure without setae. Posterior to dorsal inner corner of incisure with 1 seta, double type. Sclerotized ridge (list) dorsal to incisure forming an angular shape within rostrum (point of angle near rostral tip), more strongly sclerotized section nearest incisure (Fig. 2A). Sclerotization of rostrum very strong, resulting in external lateral processes on rostrum. Anteroventral infold, near inner corner of incisure, with 6, medium length, double setae; posterior edge of carapace infold without setae. Infold parallel to anteroventral/ventral margin with 26 setae, double type, 4 of these setae in the region ventral to incisure, diminishing in length posteriorly; 1 seta anterior to anteroventral/ventral row, no setae posterior to row. Left valve with 30 setae parallel to anteroventral/ventral margin. In vicinity of keel, list remains constant in width, forming a shallowly curved narrow smooth ridge; keel infold simple. Ridge of keel unornamented except for minute short setae or papillae emerging from unrimmed pores, and without setae; list of left valve ending in pronounced dorsal knob, without processes. Right valve with posterior margin of keel possessing no setae, with few minute setae or papillae emerging from pores; dorsal margin of keel with pronounced projection.

Lamellar prolongation of *selvage*: narrow along rostrum; along lower margin of incisure selvage is broad and striated; along ventral margin selvage is narrower, terminating posteroventrally. "Coelotrichs" (sensilla consisting of a spherical evagination of the epicuticle and a fine "hair"; Parker, submitted) (Figs 1C; 4D,F) forming rows near carapace margins present: 5–6 in rostral row, 4–5 in incisure row (Fig. 2A), 32–34 in ventral row, 5–6 in keel row; total of 46–51.

FIRST ANTENNA (Fig. 2I). *First article* bare. *Second article* with medial fine spines forming rows, and spines on ventral and dorsal margins. *Third article* very short and slightly trapezoid, without medial spines, setae of 3rd and 4th articles ringed with short spines; third article with 1 slightly longer and stouter ventral seta, distally, and 1 dorsal seta, just proximal to middle. *Fourth article* with 1 dorsal seta, longer than dorsal seta of 3rd article, and 1 ventral

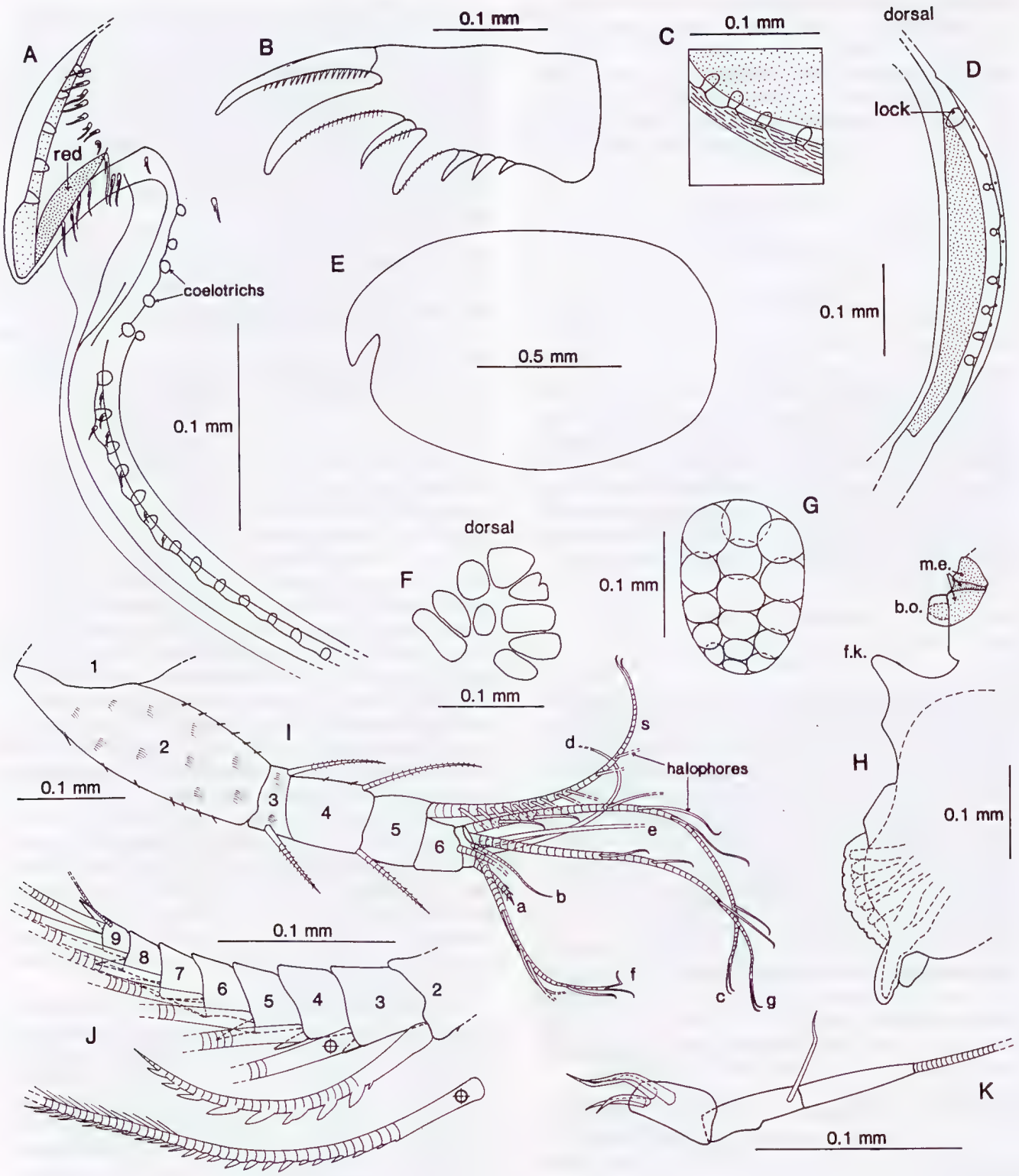

Fig. 2. *Lowrya taiti*, adult female (AM P44618). **A**, anterior of right carapace valve, medial view (area of sclerotization shaded). **B**, left furcal lamella, lateral view. **C**, appearance of coelotrichs (in anteroventral section of left carapace valve) at 200 times magnification, lateral view (setae not visible). **D**, posterior (keel) of right carapace valve, medial view. **E**, right carapace valve, medial view. **F**, central adductor muscle scars of right carapace valve, medial view. **G**, left lateral (compound) eye, lateral view (dorsal above). **H**, anterior of body, limbs removed, showing medial eye (m.e.), Bellonci organ (b.o.), frontal knob (f.k.), and upper lip. **I**, right 1st antenna, medial view. **J**, exopodial articles 2–9 of left 2nd antenna, including seta of 3rd article, medial view. **K**, endopodite of right 2nd antenna, medial view.

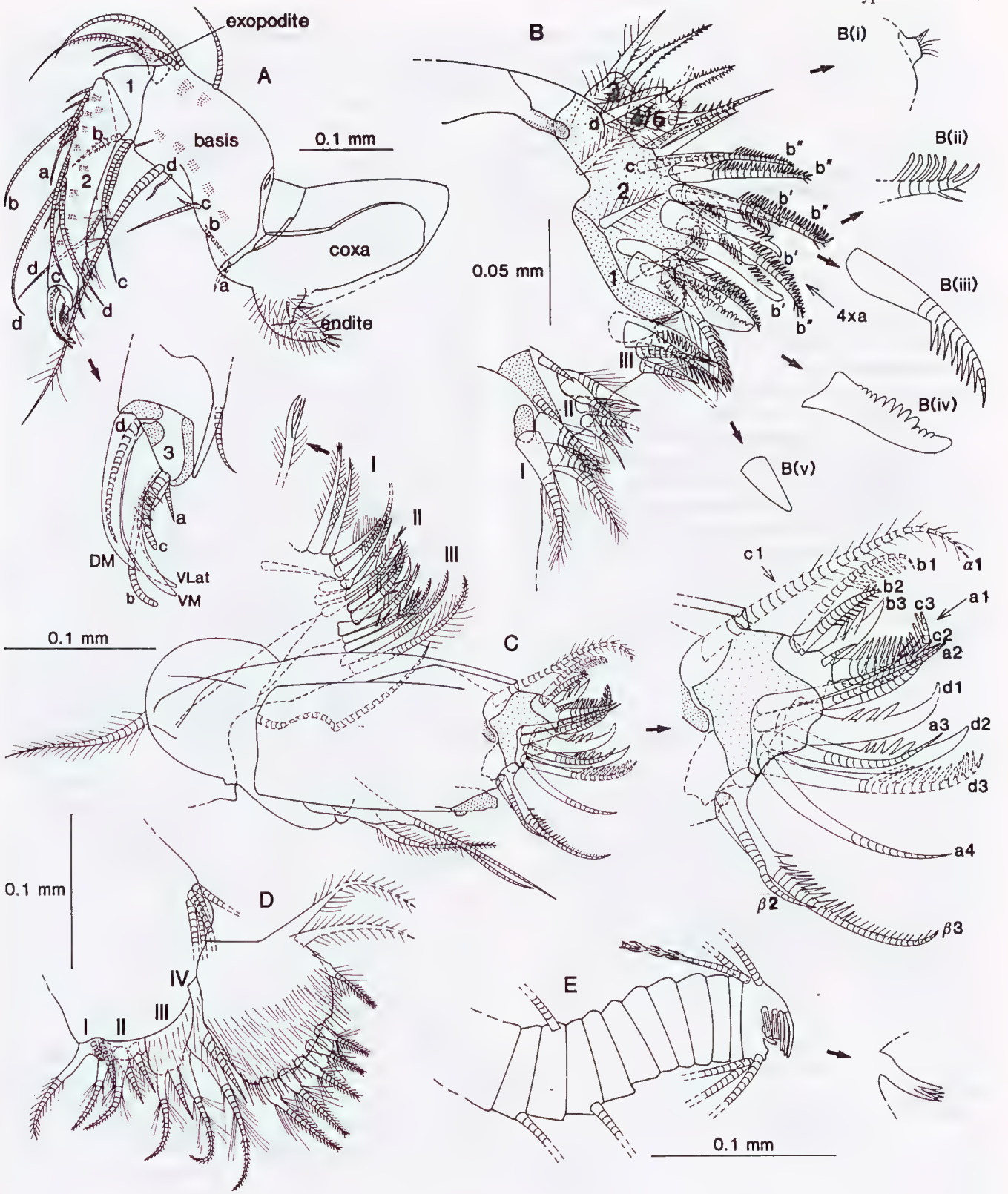

Fig. 3. *Lowrya taiti* adult female (AM P44618). **A**, right mandible, medial view. **B**, terminal part of 5th limb, anterior view, showing endites (I, II and III), and exopodial articles (1–5). **B(i)**, terminal process of 5th exopodial article. **B(ii)**, terminal part of 2nd b"-seta. **B(iii)**, longest a-seta. **B(iv)**, longest "tooth". **B(v)**, peg. **C**, right 4th limb, medial view. **D**, right 6th limb, lateral view, showing endites (I–IV). **E**, terminal part of 7th limb, showing peg.

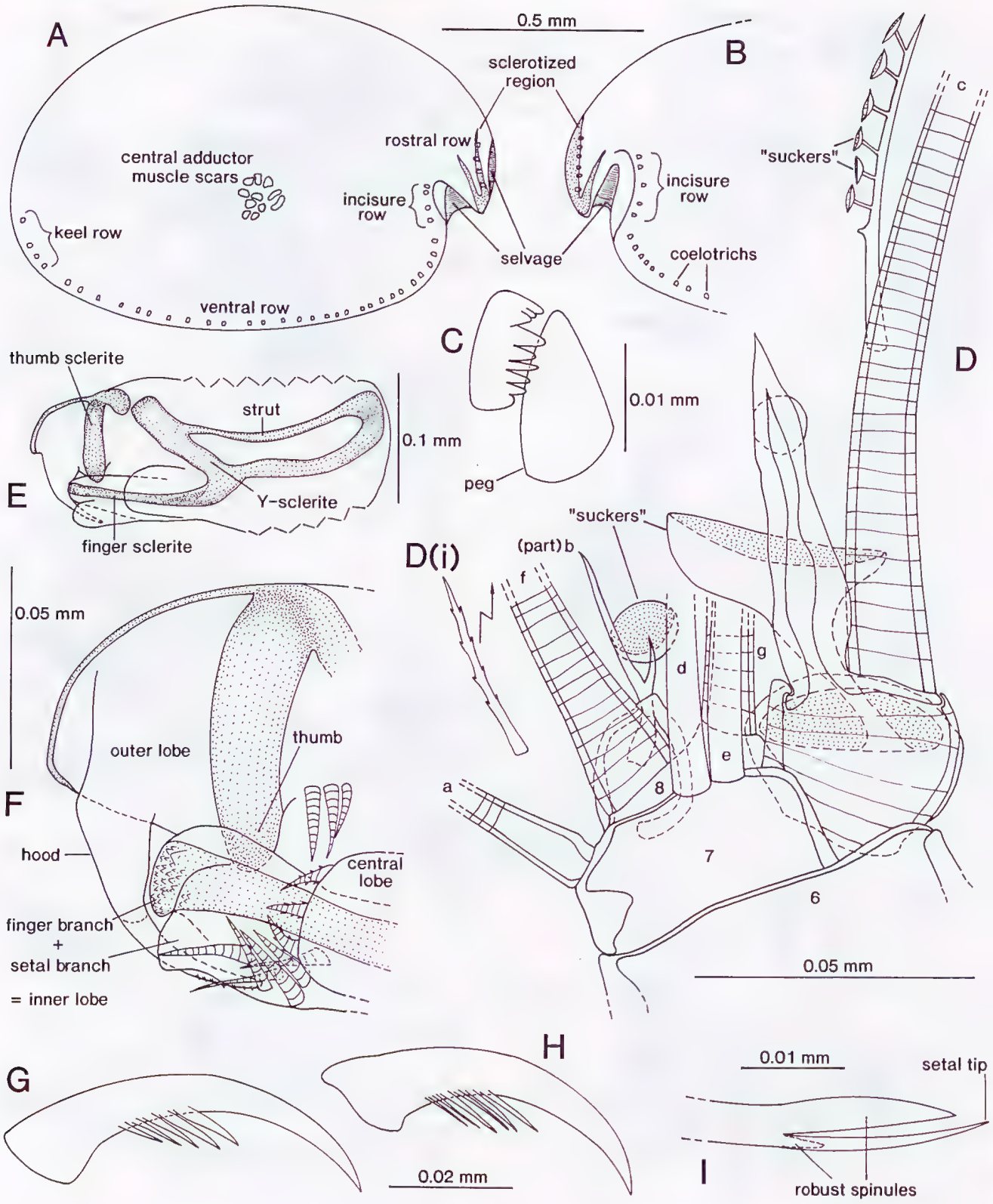

Fig. 4. *Lowrya taiti* adult male (AM P44619). **A**—left carapace valve, medial view, showing rows of coelotrichs. **B**—anterior of right carapace valve, medial view. **C**—smallest "tooth" and peg of left 5th limb, anterior view. **D**—terminal part of right first antenna, lateral view, shaft of b-seta missing. **D(i)**, 3rd most proximal halophore of the f-seta. **E**—left copulatory "limb", ventral view, showing internal sclerites. **F**—terminal part of left copulatory "limb", ventral view. **G**—VM claw of right mandible, lateral view. **H**—VLat claw of right mandible, lateral view. **I**—terminal part of seta of 2nd exopodial article of the right 2nd antenna, lateral view, showing small medial spine.

seta, sub-terminally, longer than ventral seta of 3rd article. *Fifth article*: s-seta with 10 proximal halophores, halophores long and bare; distally 2 non-terminal halophores, more slender and shorter (note that halophores are generally short for Cypridinidae). *Sixth article* with short bare and ringed medial seta near dorsal margin. *Seventh article*: a-seta short (shorter than seta of 6th article), stout and ringed with few distal spines; b-seta short, thin, ringed and bare; c-seta long and ringed, with 6 non-terminal halophores, halophores slender and bare. *Eighth article*: d- and e-setae (including terminal halophores) much longer than b-seta, bare and filamentous; f-seta shorter than c-seta, with 4 non-terminal halophores, halophores bare; g-seta of similar length to c-seta, with 3 non-terminal halophores, halophores bare. Bifurcate tips (2 terminal halophores) present on c-, f-, g- and s-setae.

SECOND ANTENNA. *Endopodite* with 3 articles (Fig. 2K). *First article* with 4 proximal setae; 2 short, 2 long. *Second article* elongate, with terminal long bare seta. *Third article* longer than 2nd article; terminal seta very long. *Exopodite* (Fig. 2J): *second article* bearing seta with tip reaching to about article number 8, bearing 9 ventral robust spinules, of which most proximal robust spinule is much smaller than others, and no dorsal spinules; medium-short thin spine on ventral margin of article. *Articles 3–8* with basal robust setae, robust seta of 5th article longest, and with natatory setae with many setules, broad setules present on seta of 3rd article only; ventral broad setules of seta of 3rd article short and stout proximally, becoming thin setules distally. Lateral robust seta of *ninth article* of similar length to that of fifth article. Ninth article with 4 setae; 2 long with many setules; 1 thinner, shorter and bare; 1 very short, thin and bare.

MANDIBLE (Fig. 3A). *Coxal endite* spinous; seta near base short, ringed and bare; 2 terminal setae, ringed and bare. Setae on ventral margin of *basis*: longest medial a-seta short-medium long and bare, and about 2 times longer than shortest seta; shortest a-seta bare; lateral b-seta medium length and bare, positioned closer to c-setae than a-setae; longest c-seta long and bare; shortest c-seta short and bare; longest d-seta much longer than basis, with rings of long spinules; shortest d-seta much less than 0.5 times length of basis, and bare; space between c- and d-setae much larger than space between c-setae. Distal part of dorsal margin of basis with 3 setae; 1 more proximal seta, medium length and bare, and 2 subterminal setae, subequal in length, long with short spinules. *Exopodite* of similar length as 1st endopodial article; medial surface smooth; dorsal process with few short spines, extending to a rounded tip, and with 2 ventral setae, of which the proximal seta is long, with short spinules. *Endopodite*: *First endopodial article* with 3 ventral setae; a-seta absent, b-seta medium length with many fine spinules, c-seta long and bare, d-seta long with rings of long spinules. *Second endopodial article* long, thin, and slightly tapered; spines (in rows) on medial surface are short and straight or slightly crescent shaped; dorsal margin with 11 setae; 1 a-, 1 b-, 1 c-, 2 d-setae; d-setae longest; d-setae long with short spinules; 5 dorsomedial shorter setae, of which there are no short, stout and unringed medial setae with long stout spinules; and 1 seta distal to d-setae. Ventral margin with few short spines, and 3 setae proximal to finger seta; no very short fine setae on ventral margin at base of finger. Finger seta about 60% length of finger. Finger long, slender with wide base, curved with rounded tip and unringed. *End article* with 3 claws; claws all similarly curved and of approximately equal length; longest claw longer than finger; DM (dorsomedial) claw shortest and thinnest, tapered, with an almost pointed tip, without spinules; VM (ventromedial) claw longest, proximally stout, distally tapered, with a rounded tip, bearing 1 minute spinule; VLat (ventrolateral) claw slightly shorter than VM claw, proximally stout, distally tapered, with a rounded tip, bearing 5 very long spinules. End article with 4 setae; ventromedial a-seta short, tapered, with an almost pointed tip; ventrolateral b-seta very long, untapered, with a rounded tip; ventromedial c-seta medium length, broad and slightly tapered, with a rounded tip; dorsolateral d-seta long, tapered, with an almost pointed tip; b-seta longest; a-seta shortest.

FOURTH LIMB (Fig. 3C). *Endite I* with 9 setae; *endite II* with 5 setae; *endite III* with 4 setae; trifid tips present on a few endite setae. *Coxa* with long dorsal seta with many setules. *Basis* with no lateral setae, and 2 medial setae. *Exopodite* bare, with 1 proximal seta, which is long with many setules; and 2 terminal setae, which are long with proximal robust setules. *Endopodite*: *first endopodial article* approximately rectangular, and bare; cutting tooth large, with 3 cusps, cusps squarish in shape, partial suture or cutting edge separating proximal part from rest of cutting tooth present. 1 α-seta; α1-seta very long with distal setules. 2 β-setae; β2-seta medium length and bare, β3-seta very long and denticulate. *Second endopodial article* much narrower than 1st article, with 4 a-setae: a1-seta thin with a widened base, medium length and bare, distally ringed; a2-seta thin with a widened base, long and bare, ringed throughout most of length; a3-seta thin with a widened base, long and bare, ringed throughout most of length; a4-seta thin with a widened base, long and bare, distally ringed. 3 b-setae: b1-seta medium width, medium length, ringed throughout most of length, with 6 denticles, denticles medium broad, of medium length and present distally; b2-seta medium width with a widened base, medium length, unringed, with 11 denticles, denticles narrow, short and present distally; b3-seta (most posterior) claw-like, medium length, unringed, with 2 denticles, denticles very broad, long and present centrally. 3 c-setae: c1-seta (most anterior) very thin, short and bare, ringed throughout most of length; c2-seta broad, medium length, ringed throughout most of length, with 10 denticles, denticles medium broad, long and present along most of setal length; c3-seta broad, long and spinous, ringed throughout most of length, with 10 denticles, denticles medium broad, long and present along most of setal length. 3 d-setae: d1-seta claw-like, long, unringed, with 3 denticles, denticles very broad, of medium length and present centrally; d2-seta claw-like, long, unringed, with 5 denticles, denticles broad, long and present centrally, of these denticles 2 are large, and positioned distally on the anterior side of the d2-seta; d3-seta thin with a widened base, long, distally ringed, with 10 denticles, denticles

medium broad, long and present distally, of these denticles 2 are large, and positioned proximally on the anterior side of the d3-seta.

FIFTH LIMB (Fig. 3B). With 40 *epipodial setae*. Anterior distal tooth of *Protopodite* with rounded tip. *Endite I* with 6 setae; *endite II* with 6 setae; *endite III* with 6 setae. *First exopodial article*: posterior row of 6 pectinate teeth (claw-like setae); tooth 1 (smallest, most posterior) with 7 denticles, tooth 2 with 7 denticles, tooth 3 with 8 denticles, tooth 4 with 9 denticles, tooth 5 with 10 denticles, tooth 6 with 12 denticles; peg large, and triangular; peg-seta medium length, stout, and with setules throughout length, peg-seta about same length as longest tooth. Anterior side of article with row of 3 setae; 1st-seta (inner) medium length, medium width, and with setules throughout length; 2nd-seta long, medium width, and with distal setules; 3rd-seta long, medium width with a broadened base, with many setules and distal spinules. Additionally 1 more proximal anterior seta on 1st exopodial article, close to protopodite; proximal anterior seta medium length, thin, and with setules throughout length. *Second exopodial article*: with 4 a-setae, a-setae claw-like, ringed, and coarsely denticulate; 7 b-setae, b-setae medium length to long, and most ringed (posterior row of 3 b'-setae, anterior row of 4 b"-setae); posterior c-seta ringed throughout most of length, and with distal spinules; anterior d-seta unringed with many setules. Inner lobe of *third exopodial article* with 3 setae; most proximal seta very short, unringed, and bare; subterminal seta long, distally ringed, and bare; terminal seta medium length, distally ringed, and bare. Outer lobe of 3rd exopodial article hirsute with 2 medium broad setae; outer seta medium length, unringed, and with proximal setules. *Fourth* and *fifth exopodial articles* fused and hirsute. Fourth article with 1 medium broad seta. Fifth article with 2 medium broad setae, subequal in length, unringed, with many spinules. Terminal process on inner 5th article medium sized with long spines and a group of spines forming a triangular sub-process.

SIXTH LIMB (Fig. 3D). With 5 setae in place of *epipodite*; these setae are bare and ringed. *Endites* with medial setae. Endite setae: *I* = 3; 1 long, distally ringed, with short distal setules, and without robust setules; 2 very short, medium width, ringed, with short setules, without robust setules. *II* = 5 setae; 2 long, distally ringed, with long proximal setules and short distal robust setules; 3 medium short, medium width with broad base, ringed, with long setules, without spinules. *III* = 3 setae; 2 long, distally ringed, with long proximal setules and short distal robust setules; 1 medium short, thin with broad base, ringed, with long proximal setules and without robust setules. *IV* = 2 setae; 1 very long, distally ringed, with long central setules and short distal robust setae; 1 medium long, thin with broad base, ringed, with long central setules and without robust setae. Endites separated from each other and rest of limb by sutures or grooves. *Terminal article* approximately square shaped, basally separated by suture or groove from rest of limb; medial surface hirsute; lateral surface with rows of stout long setae along ventral margin. 5 anterior ventral terminal setae, with broad bases abruptly constricting to a narrow distal width, distally ringed, with long proximal setules and long distal spinules; setae of terminal article reducing evenly in length from most anterior seta to most posterior, with bases on margin of article; gap posterior to anterior ventral terminal setae long, including a rounded corner and a small anterior recess, gap = about 40% ventral length of terminal article, followed by 3 posterior setae, mostly unringed, some with bases on edge of article, some with bases set back from edge, the longest is the most posterior; the most anterior is medium length, with a broad base abruptly constricting to a narrow distal width, with long proximal setules and long distal spinules.

SEVENTH LIMB (Fig. 3E). Total of 9 setae. *Comb side* with 1 nonterminal seta, and 3 terminal setae; minimum number of bells on setae = 4, maximum number of bells on setae = 6. *Peg side* with 2 nonterminal setae, and 3 terminal setae; minimum number of bells on setae = 4, maximum number of bells on setae = 6. *Comb* of 3 long teeth on each side, coarsely denticulate, with rounded tips, central tooth slightly longer than others; 2 short teeth on each side, medium length, with square tips, and deep grooves. *Peg* medium length, slightly curved, narrow; tip of peg similar width to centre of peg, with many points; base of peg recessed from outer limb edge.

FURCA (Fig. 2B). Left lamella with 7 claws, right lamella with 7 claws; claws 2 and 4 fused to lamella; claw 3 shorter and thinner than claw 4; claw 1 long and medium wide; claw 4 exceptionally broad; claw 5 short and thin; anterior claws short and thin; claws generally increasing in size posteriorly (with exception). Claws generally evenly curved, four most posterior claws with spinules; distal medial robust setules of most posterior claw absent. Lamellae elongate, tapered and bare.

ANTERIOR OF BODY (Fig. 2H). *Bellonci organ*: shape (non-extended) is square; length (non-extended) = 0.03 mm; width similar to length; slightly pigmented.

Eyes: *medial eye* (Fig. 2H) medium sized; length = 0.04 mm; pigmented. *Lateral eye* (Fig. 2G): length = 0.18 mm; large (about 20 times size of medial eye); broadest dorsally; with at least 16 ommatidia, largest ommatidia located dorsally; ommatidia light amber in transmitted light, pigment between ommatidia maroon in transmitted light.

Upper lip (Fig. 2H): single undivided anterior part directed anteroventrally, ventral field of anterior part pear-shaped, with about 18 valves; valves large, and arranged in about 3–5 anterior-posterior rows on a single plane; anterior part bare. Pair of lateral *tusks* short, medium width with parallel margins, each with 1 valve, valves medium sized, positioned terminally; tusks not hirsute; spurs on tusks absent; tusks terminating at a rounded posterior corner. Upper lip pigmented.

Frontal knob (Fig. 2H): very elongate, rounded, width less than length; without projections ventral to frontal knob.

POSTERIOR OF BODY. Dorsal folds absent. *Y-sclerite* with ventral branch shorter than 50% length of dorsal branch.

Description of adult male characters

Most characters common to both sexes have been omitted from the following description.

CARAPACE (Fig. 4A,B). Length = 1.12–1.20 mm (number of specimens examined = 9), height = 0.80 mm; length/height = 1.5. Coelotrichs: 4 in rostral row, 3 in incisure row, 27 in ventral row, 4 in keel row; total of 38.

FIRST ANTENNA (Fig. 4D). *Fifth article*: s-seta with 8 bare proximal halophores (most proximal 6 halophores longest and separated by a small gap from more central 2 halophores), and 2 shorter, bare, distal non-terminal halophores. *Seventh article*: b-seta with basal setule with bulbous base, large proximal "sucker" (transparent), without non-terminal halophores, additionally 2 setules present, each bearing 7 small "suckers", small process just proximal to most proximal "sucker" present; c-seta with bulbous base with large basal setule with sub-terminal process, and additional cup-shaped basal process from which a large "sucker" (diameter greater than width of each of the distal five articles; transparent) arises, 6 short and slender non-terminal halophores, additionally 2 proximal setules, each bearing 6–7 small "suckers", small process just proximal to most proximal "sucker" present. *Eighth article*: f-seta with 5 non-terminal halophores, with short spinules; g-seta with 11 non-terminal bare halophores.

COPULATORY "LIMB" (Fig. 4E,F). *First article*: *Y-sclerite* prominent; *strut* present so that the sclerite forms an irregular rectangular loop; loop broader distally; *finger sclerite* medium wide, terminating at distal tip of finger branch. *Inner lobe* elongate with rounded tip. *Finger branch* and *setal branch* separated by a deep terminal cleft; tip of finger branch with many minute scales. Terminal and cleft region of setal branch bears minute scales; external surface of setal branch with 6 setae, ringed and bare. *Outer lobe* with *thumb sclerite* terminating at dorsal hood edge; *thumb* small and bare, located proximally on thumb sclerite, near hood; thumb with 3 ringed, bare setae, located proximal to tip of thumb sclerite. *Hood*: dorsoventral margin medium length, distally triangular, with an anterior step-like constriction, becoming a finger-like lobe; length of anterior peak small; tip of hood complete, with few minute scales or spines. Hood extends less than half way over inner lobe. *Central lobe*: width about equal to length; length = about 50% of that of inner lobe. The central lobe bears 3 terminal setae, which are ringed with spinules.

ANTERIOR OF BODY (Fig. 5A). *Lateral eye*: very large, length = 0.20 mm; broadest dorsally; at least 16 ommatidia (7 large, of approximately equal size; about 9 small, of approximately equal size), largest ommatidia located dorsally.

Etymology. This species is named in honour of Noel N. Tait, invertebrate zoologist, who provided the author with much invaluable advice on zoological subjects.

Lowrya kornickeri n.sp.

Figs 5–7

Type locality. Collected from east of Grotto Point, Port Jackson, NSW, Australia (33°49.05'S 151°15.92'E); baited trap set overnight at 11 m depth. Collected by P. Berents, A.R. Parker, K.B. Attwood and A. Murray on M.V. Sula, 25–26 November 1993. In addition to *Lowrya kornickeri* unidentified cirolanid isopods and lysianassoid amphipods were caught. Only a small (representative) proportion of this trap sample was made available (this study was not the primary purpose of the trapping), therefore relative abundances are unknown. No adult females are known.

Type material. HOLOTYPE: AM P45463, adult male. PARATYPES: AM P45465, adult male; AM P45464, juvenile (A-1) female; AM P42244, adult male; BMNH 1995:1603, adult male (undissected); NMNH, adult male (undissected).

Description of adult male characters

COLOUR OF LIVING OSTRACODS. Beige with a red area above the incisure when viewed from certain directions.

CARAPACE. Length = 1.24 mm, height = 0.82 mm; length/height = 1.51. Range of length = 1.22–1.28 mm (number of specimens examined = 4).

Shape (Fig. 6A): rectangular oval, very slightly protruding keel; margins slightly rounded, posterodorsal margin more steeply sloped than anterodorsal margin. Keel joined to curved posterior margin of valve by smooth convex curve; dorsal edge of keel slightly below midheight of valve; dorsal edge of incisure slightly overlapping ventral edge at inner end, prominent line on outer surface of valve curving from inner dorsal edge of incisure to anterior margin of valve (ventral to incisure). Tip of rostrum rounded, with few small anterior bumps.

Valve surface: smooth at low magnification, but with faint scale-like pattern visible on anterior margins with light microscope at 100×; setae on valve surface medium sized and scattered evenly; 9 *muscle scars*, forming a circle.

Infold (Fig. 6B): infold posterior to rostrum with row of 8 setae, double type, at an angle to valve margin, all dorsal to incisure; no setae anterior or posterior to carapace infold row. Dorsal edge of incisure with 4 single setae. Dorsal to dorsal inner corner of incisure with 1 double seta, at an angle with incisure margin. Sclerotized ridge (list) dorsal to incisure at an angle with incisure margin; sclerotization strong, causing red colouration from certain directions (after preservation) of dorsal incisure margin. Anteroventral infold, near inner corner of incisure, with 5 double setae (2 medium length, 3 short); posterior edge of carapace infold without setae. Infold parallel to anteroventral/ventral margin with 21 double setae; 3 in the region ventral to incisure; diminishing in length posteriorly; no setae anterior or posterior to anteroventral/ventral row. List becomes broader in vicinity of keel, forming a shallowly curved wide smooth ridge; keel infold simple. Ridge of keel unornamented except for minute

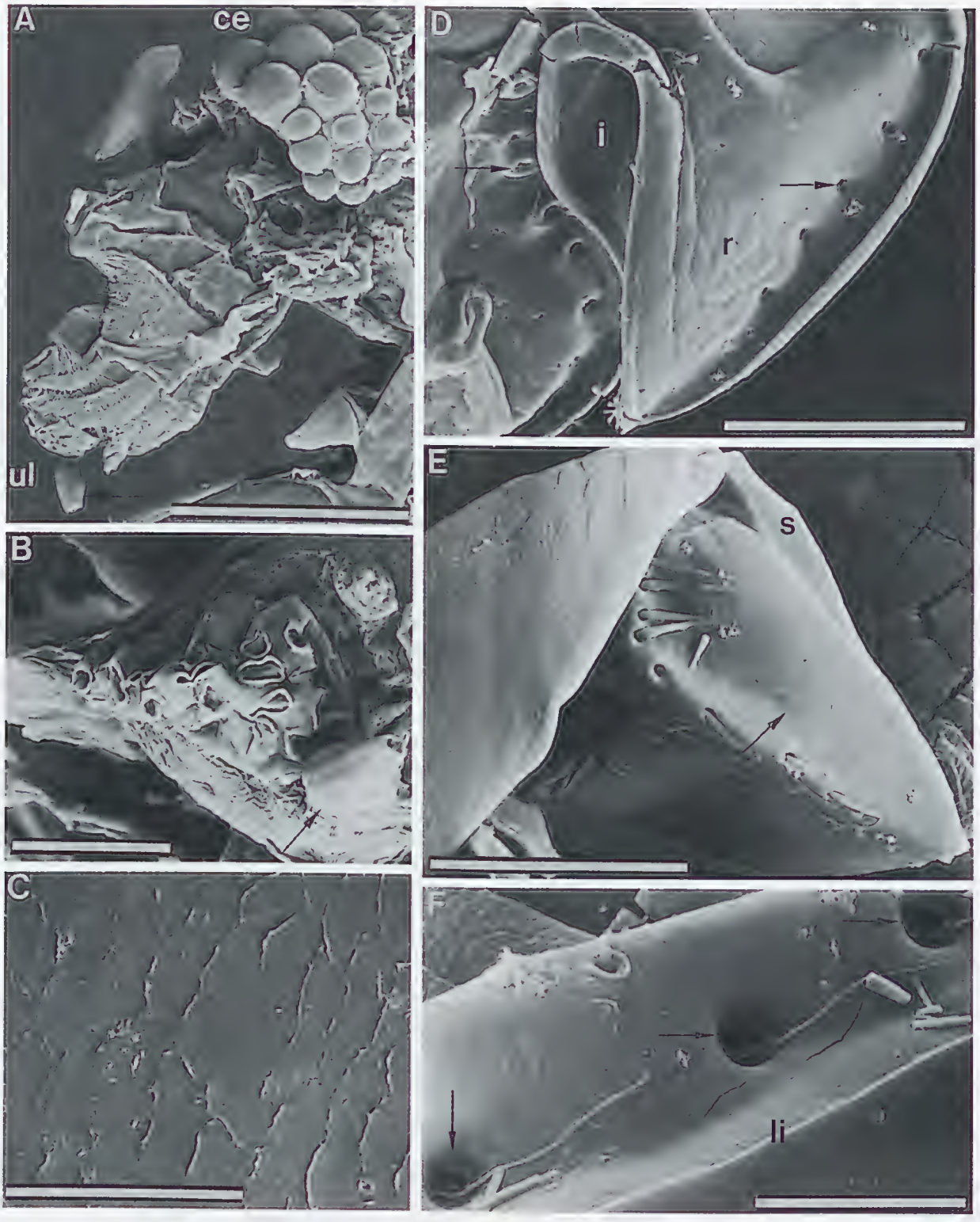

Fig. 5. *Lowrya taiti* Scanning electron micrographs, adult male (AM P45532). **A**, anterior of body, limbs removed, showing upper lip (ul) and compound eye (ce); right tusk arrowed, left tusk broken. **B**, upper lip, ventral view (right tusk arrowed). **C**, surface of right carapace valve, central region (anterior to the right), lateral view. **D**, rostrum (r) and incisure (i) of the right carapace valve, lateral view; examples of coelotrichs arrowed. **E**, rostrum of right carapace valve, medial view, showing internal setae, selvage (s) and sclerotized region (inner edge of "angle" arrowed); sclerotized region remains rigid while remaining carapace has curled after drying. **F**, three coelotrichs (arrowed) of the ventral row (anterior part) of the left carapace valve, also showing recessed "lip" near edge of valve (l), and a more common type of external carapace seta (distributed randomly over entire surface). Scales: **A** = 0.2 mm; **B** and **C** = 50 μm; **D** and **E** = 0.1 mm; **F** = 20 μm.

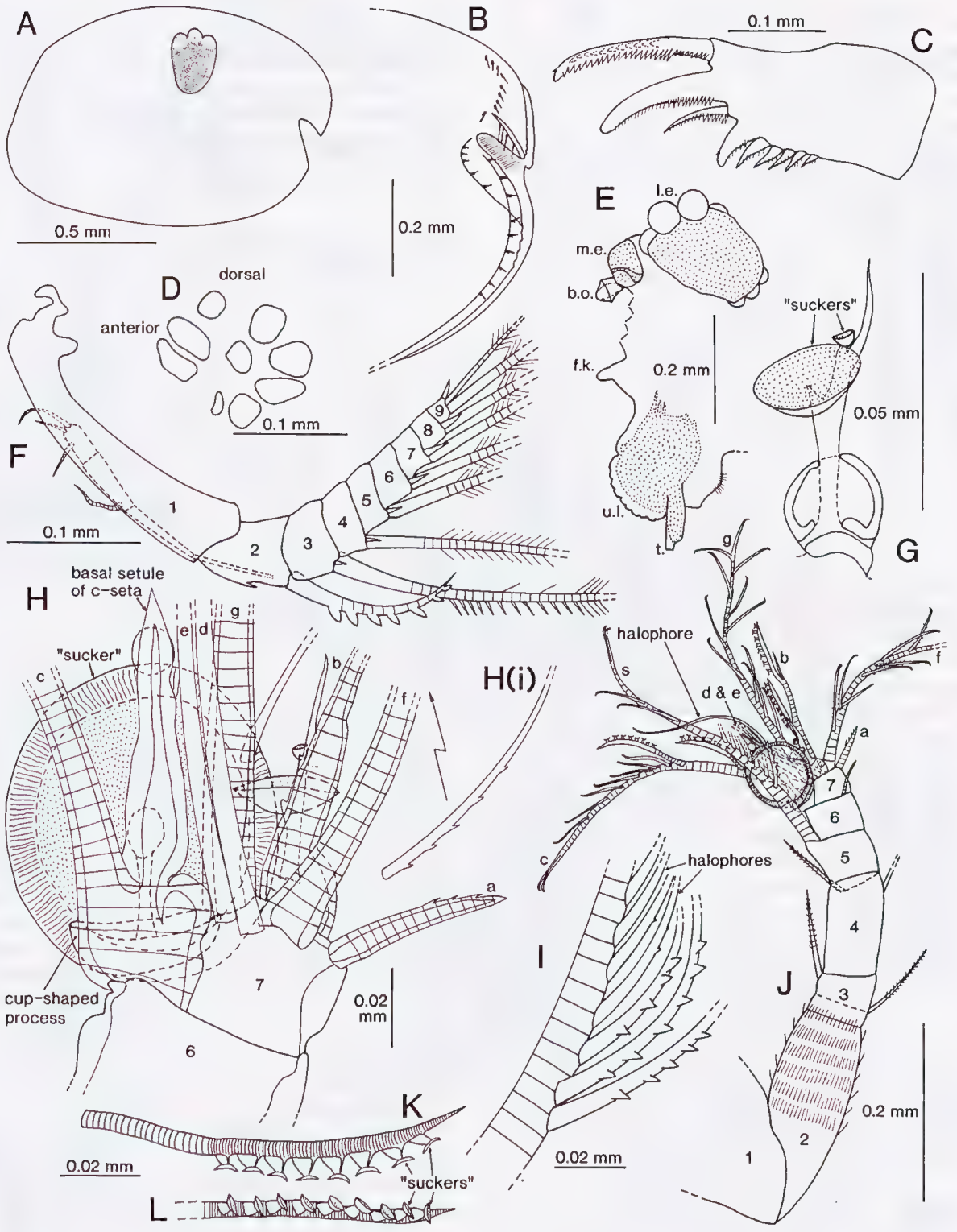

Fig. 6. *Lowrya kornickeri* adult male (AM P45463). **A**, whole animal, lateral view. **B**, anterior of left carapace valve, medial view. **C**, left furcal lamella, lateral view. **D**, central adductor muscle scars of right carapace valve, medial view. **E**, anterior of body, limbs removed, showing medial eye (m.e.), lateral eye (l.e.), Bellonci organ (b.o.), frontal knob (f.k.), and upper lip (u.l.) including left tusk (t.), areas of maroon pigmentation shaded. **F**, endopodite (dashed) and exopodite of left 2nd antenna, lateral view. **G**, basal setule of b-seta of right 1st antenna, bearing 2 "suckers", medial view. **H**, terminal articles of left 1st antenna, s-seta not illustrated, 8th article not visible, lateral view. **H (i)**, proximal section of 7th most proximal halophore of the f-seta of the left 1st antenna, lateral view. **I**, proximal halophores arising from shaft of s-seta of right 1st antenna, medial view. **J**, right 1st antenna, medial view. **K**, 2nd most proximal setule of the c-seta of the left 1st antenna, showing "suckers", lateral view. **L**, distal part of 2nd most proximal setule of the b-seta of the left 1st antenna, showing "suckers", dorsolateral view.

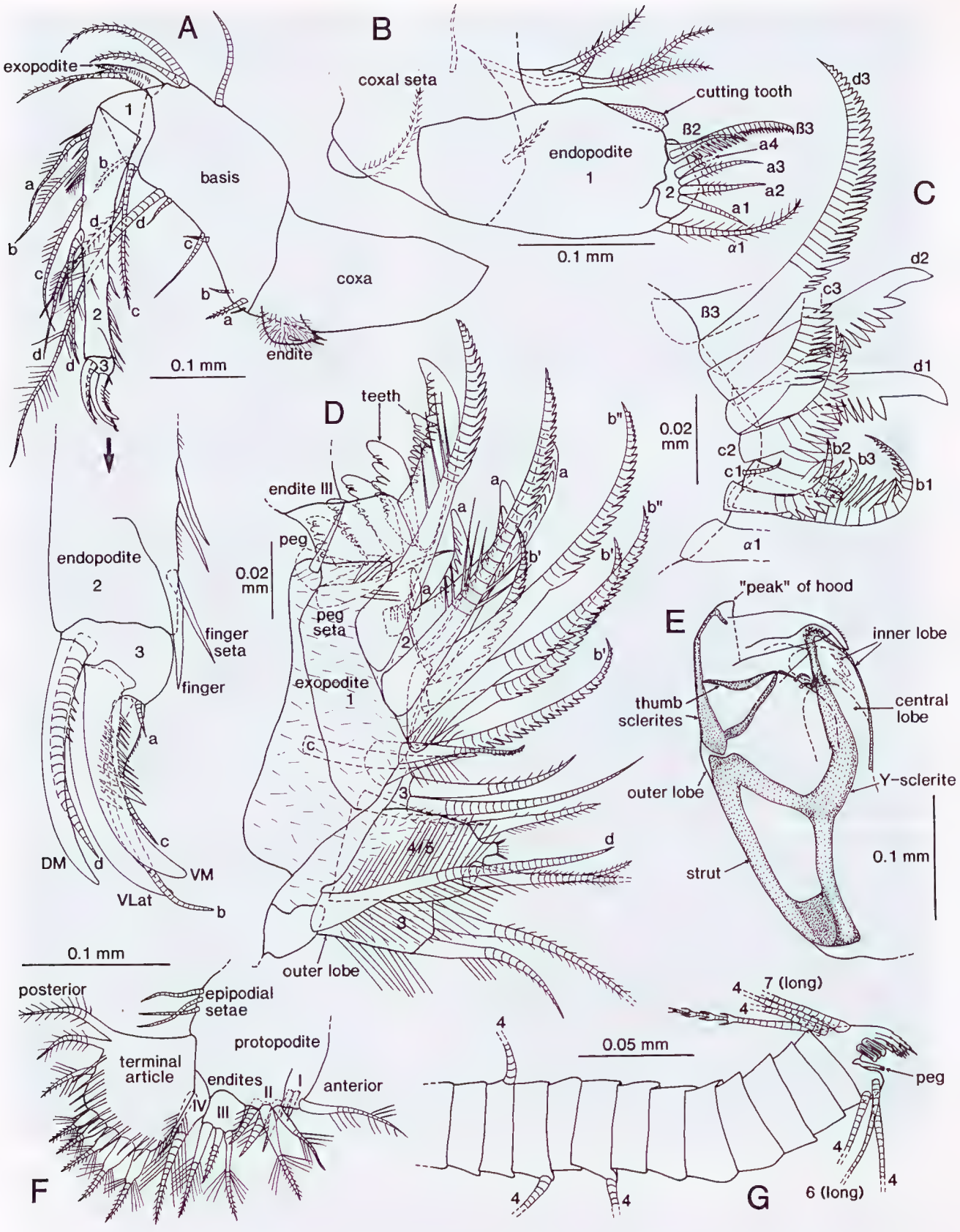

Fig. 7. *Lowrya kornickeri* adult male (AM P45463). **A**, right mandible, medial view. **B**, left 4th limb, showing some terminal endopodial setae, lateral view. **C**, terminal endopodial setae of right 4th limb excluded from **B**, medial view. **D**, terminal section of exopodite of right 5th limb, anterior view (the spines of many setae are longer than appear in this illustration, due to the angle of observation). **E**, left copulatory "limb", dorsal view. **F**, right 6th limb, lateral view. **G**, terminal section of 7th limb.

short setae or papillae emerging from unrimmed pores, without setae; list of left valve without dorsal knob, and without processes. Right valve with posterior margin of keel without setae, with few papillae emerging from pores; dorsal margin of keel without process.

Lamellar prolongation of *selvage*: medium width along rostrum; very broad and striated along lower margin of incisure; narrower along ventral margin; terminating anteroventrally. Coelotrichs (evagination/"hair" sensillae; Parker, submitted) absent.

FIRST ANTENNA (Fig. 6G–K). *First article* bare. *Second article*: many medial spines forming rows, and spines on ventral and dorsal margins. *Third article*: short, without medial spines; with ventral seta of approximately equal to length of dorsal seta, positioned distally; 1 dorsal seta at base of article. *Fourth article*: 1 dorsal seta, of approximately equal length to dorsal seta of 3rd article; 1 ventral setae, positioned terminally, shorter than ventral seta of 3rd article; setae of 3rd and 4th articles ringed with short spinules. *Fifth article*: s-seta (formally the sensory seta of the fifth article; Parker, 1995, 1998) with 7 long proximal halophores (setules on the first antennae; Parker, 1995, 1998), some with proximal spinules; distally 2 non-terminal halophores, more slender and shorter (note that all halophores are generally short for Cypridinidae). *Sixth article*: short, bare and ringed medial seta near dorsal margin. *Seventh article*: a-seta medium length, stout and ringed with few distal spinules; b-seta short, with basal setule with bulbous base, large proximal "sucker" (transparent) and small distal "sucker", without non-terminal halophores, additionally 2 setules present, each bearing 8–9 small "suckers", small process just proximal to most proximal "suckers" absent; c-seta long and ringed with bulbous base with large basal setule with sub-terminal process, and additional cup-shaped basal process from which a very large "sucker" (diameter > width of each of the distal five articles; transparent) arises, with 7 short and slender non-terminal halophores, most proximal halophore with few short spinules, additionally 2 proximal setules present, each bearing 8 small "suckers", small process proximal to most proximal "sucker" absent. Small "suckers" on the non-basal setules of the b- and c-setae bear widened, almost cone-shaped, shafts. *Eighth article* (very reduced or absent): d- and e-setae (including terminal halophores) longer than b-seta, bare and filamentous; f-seta shorter than c-seta, with 8 short non-terminal halophores, most with small proximal spinules; g-seta shorter than c-seta and longer than f-seta, with 9 short non-terminal halophores, some with small proximal spinules. Bifurcate tips (2 terminal halophores) present on c-, f-, g- and s-setae.

SECOND ANTENNA. *Protopodite*: long, bare seta. *Endopodite* (Fig. 6F): 3 articles. *First article*: 3 proximal setae; 2 short, 1 long, and no distal setae. *Second article*: elongate, with terminal long bare seta. *Third article*: longer than 2nd article and narrow; terminal seta long and unringed. *Exopodite* (Fig. 6F): *second article*: bearing seta with tip reaching to about 8th article, bearing 7 ventral robust spinules, most proximal spinule is similar size to others, no dorsal spinules; medium-short thin spine on ventral margin of article. *Articles 3–8*: with basal robust setae becoming longer distally; natatory setae with many fine setules, broad setules present on seta of 3rd article only. *Ninth article*: lateral robust seta of similar length to that of 8th article; 2 setae, both long with many fine setules.

MANDIBLE (Fig. 7A). *Coxal endite*: spinous; seta near base short, ringed and bare; 2 terminal setae, unringed and bare. Setae on ventral margin of *basis*: longest medial a-seta short-medium length, with short distal spinules, about 3 times longer than shortest seta; shortest a-seta bare; lateral b-seta short and bare, positioned very close to a-setae; longest c-seta long and bare; shortest c-seta short and bare; longest d-seta much longer than basis, with rings of long spinules; shortest d-seta much less than 0.5 times length of basis, and bare; space between c- and d-setae much larger than space between c-setae. Distal part of dorsal margin of basis: 3 setae; 1 more proximal seta, medium length and bare; 2 subterminal setae, subequal in length, with short spinules. *Exopodite*: similar length as 1st endopodial article; medial surface wrinkled; dorsal process hirsute, extending to a pointed tip; with 2 ventral medium-broad setae, longest with short spinules. *Endopodite*: *First endopodial article*: 3 ventral setae; a-seta absent, b-seta medium length with spinules, c-seta long with spinules, d-seta long with rings of long spinules. *Second endopodial article*: long, very thin, and slightly tapered; spines (in rows) on medial surface are long and straight; dorsal margin with 11 setae; 1 a-, 1 b-, 1 c-, 2 d-setae; c-seta longest; d-setae long with short spinules; 5 dorsomedial shorter setae (1 short, stout and unringed with long stout spinules); 1 seta distal to d-setae; ventral margin with few long spines and 3 setae proximal to finger. Finger seta about 60% length of finger; finger long, slender with wide base, curved with pointed tip and unringed. *Terminal article*: with 3 claws; claws all similarly curved and of approximately equal length; longest claw longer than finger; DM (dorsomedial) claw shortest and thinnest, tapered, with an almost pointed tip, bearing 5 spinules of medium length; VM (ventromedial) claw midsize, proximally stout, distally tapered, with rounded tip, bearing 12 spinules (6 medium length and proximal, 6 long and more distal); VLat (ventrolateral) claw slightly longer than VM claw, proximally stout, distally tapered, with a rounded tip, bearing 12 spinules (6 medium length and proximal, 6 long and more distal); 4 setae; ventromedial a-seta short, tapered, with an almost pointed tip; ventrolateral b-seta very long, almost bulbous proximally, distally tapered, with unevenly curved tip, bearing many short spinules; ventromedial c-seta medium length, tapered, with rounded tip; dorsolateral d-seta long, tapered, with almost pointed tip; b-seta longest; a-seta shortest.

FOURTH LIMB (Fig. 7B,C). *Endite I* with at least 6 setae; *endite II* with 5 setae; *endite III* with 5 setae; trifid tips present on a few endite setae. *Coxa*: long dorsal seta with many setules. *Basis*: no lateral setae, 3 medial setae. *Exopodite*: bare; 1 proximal seta, long with many setules; 2 terminal setae, long with many setules. *Endopodite*: *first endopodial article*: approximately rectangular, uniformly spinous; cutting tooth large, with 2 squarish cusps, partial suture or cutting edge separating proximal part from rest of cutting tooth; 1 α-seta (α1), very long with many setules; 2 β-setae: β2-seta medium length and bare, β3-seta very long and denticulate. *Second endopodial article*: much

narrower than 1st article; 4 a-setae; broad with widened bases, medium long with proximal spinules, ringed throughout most of length; 3 b-setae; b1-seta medium width with widened base, long, ringed throughout most of length, with 7 long medium-broad denticles, present proximally, and about 9 smaller distal spinules; b2-seta medium width with a widened base, medium length, ringed throughout most of length, with 6 broad denticles of medium length and present centrally; b3-seta (most posterior) claw-like, medium length, unringed, with 2 long, broad denticles, present centrally; 3 c-setae; c1-seta (most anterior) very thin, short and bare, ringed throughout most of length; c2-seta medium width with widened base, medium length, ringed throughout most of length, with 16 proximal broad denticles, longer proximally; c3-seta broad, long, ringed throughout most of length, with 15 long, broad denticles, present distally; 3 d-setae; d1-seta claw-like, medium length, unringed, with 6 long, broad denticles, present centrally; d2-seta claw-like, long, unringed, with 9 long, broad denticles, present centrally; d3-seta medium width with widened base, very long, distally ringed, with 35 medium-broad denticles, medium length proximally, decreasing in length distally, present along most of setal length.

FIFTH LIMB (Fig. 7D). 38 *epipodial setae*. *Protopodite*: anterior distal tooth with rounded tip. *Endite I* with 6 setae; *endite II* with 6 setae; *endite III* with 7 setae. *First exopodial article*: posterior row of 6 denticular teeth; tooth 1 (smallest, most posterior) with 5 denticles, tooth 2 with 8 denticles, tooth 3 with 8 denticles, tooth 4 with 9 denticles, tooth 5 with 9 denticles, tooth 6 with 10 denticles; peg large, triangular; peg-seta medium length, stout, with very long, thin proximal spinules, peg-seta shorter than longest tooth; anterior side with row of 3 setae; 1st-seta (inner) short, thin with broadened base, and with very long, thin proximal spinules and long, broad distal spinules; 2nd-seta very long, medium width with broadened base, very long, thin proximal spinules and long and broad distal spinules; 3rd-seta very long, medium width with broadened base and distal spinules; additionally 1 proximal anterior bare seta, very short, medium width with broadened base, close to protopodite. *Second exopodial article*: 4 a-setae, claw-like and coarsely denticulate; 5 b-setae, medium-long to very long, ringed, posterior row of 3 b'-setae, anterior row of 2 b"-setae; posterior c-seta unringed and bare; anterior d-seta distally ringed, with very long, thin proximal spinules. Inner lobe of *third exopodial article* with 3 setae; most proximal seta short, unringed, with distal spinules; subterminal seta long, ringed and bare; terminal seta medium-long, distally ringed, with distal spinules. Outer lobe of 3rd exopodial article: hirsute, 2 medium-broad setae; outer seta medium-long, distally ringed, with long thin proximal spinules and short thin distal spinules along outer margin only. *Fourth* and *fifth exopodial articles* fused and hirsute. *Fifth article*: 2 setae, subequal in length, ringed, with many short setules; terminal process large with long spines. *Fourth article*: 1 seta.

SIXTH LIMB (Fig. 7F). 3 bare and ringed setae in place of *epipodite*. *Endites* with medial setae, separated from each other and rest of limb by sutures or grooves (except endites I and II, which are fused to rest of limb). Endite setae: *I* = 3; 1 very long, distally ringed, with long setules; 2 very short, medium width, ringed, with long setules and without spinules; *II* = 5; 2 long, distally ringed, with long central setules and short distal spinules; 3 medium short, medium width with broad base, ringed, with long setules; longest with short distal spinules; *III* = 3; 2 long, distally ringed, with long central setules and with short distal spinules; 1 medium short, medium width, ringed, without setules and with short spinules; *IV* = 2, 1 very long, ringed, with long central setules and with short distal spinules; 1 short seta, medium long, thin with broad base, distally ringed, with long central setules and without spinules. *Terminal article*: approximately square shaped, basally separated by suture or groove from rest of limb; medial surface hirsute; lateral surface with rows of long spines; 5 anterior ventral terminal setae, with broad base abruptly constricting to narrow distal width, distally ringed, with long central setules and long distal spinules, reducing evenly in length from most anterior seta to most posterior, with bases on margin of article; gap posterior to anterior ventral terminal setae medium length, including rounded corner, gap = about 20% ventral length of terminal article, followed by 3 ringed posterior setae, some with bases on edge of article, some with bases set back from edge, longest is posterior, most anterior setae long, with broad base abruptly constricting to a narrow distal width, with long central setules and long distal spinules.

SEVENTH LIMB (Fig. 7G). Total of 10 setae. *Comb side*: 1 nonterminal seta, 4 terminal setae; minimum number of bells on setae = 4, maximum number of bells on setae = 7. *Peg side*: 2 nonterminal setae, 3 terminal setae; minimum number of bells on setae = 4, maximum number of bells on setae = 6. *Comb*: 3 long teeth on each side, long teeth long, coarsely denticulate, with pointed tips, central long tooth longer than others; 2 short teeth on each side, short teeth medium long, with square tips, and deep grooves. *Peg*: long, slightly curved, very narrow; tip of peg similar width to centre of peg, and with many points; base of peg recessed from outer limb edge.

COPULATORY "LIMB" (Fig. 7E). *First article*: *Y-sclerite* prominent; *strut* present so that sclerite forms an irregular rectangular loop; loop broader distally; *finger sclerite* broad proximally, becoming narrow distally, forming a continuous section along inner margin of inner lobe, terminating near base of inner lobe. *Inner lobe*: elongate with rounded tip. *Finger branch* and *setal branch* separated by a deep terminal cleft. *Finger branch*: tip with stout spines; terminal and cleft region bare. *Setal branch*: external surface with 2 bare, ringed setae. *Outer lobe*: *thumb sclerite* forming edge of a triangle with an extended tip; *thumb* small and bare, located proximally on thumb sclerite, near hood; 2 bare, ringed setae located proximal to tip of thumb sclerite. *Hood*: dorsoventral length medium long; distally triangular becoming a finger-like lobe; anterior peak short; tip of hood complete, with few minute scales or spines; hood extends almost entirely over inner lobe. *Central lobe*: width approximately equal to length; length = about 50% of that of inner lobe; 3 terminal ringed and setae with many spinules.

FURCA (Fig. 6C). Left lamella with 9 claws, right lamella with 9 claws; claws 2 and 4 fused to lamella; claw 3 longer but thinner than claw 4; claw 1 long and medium wide;

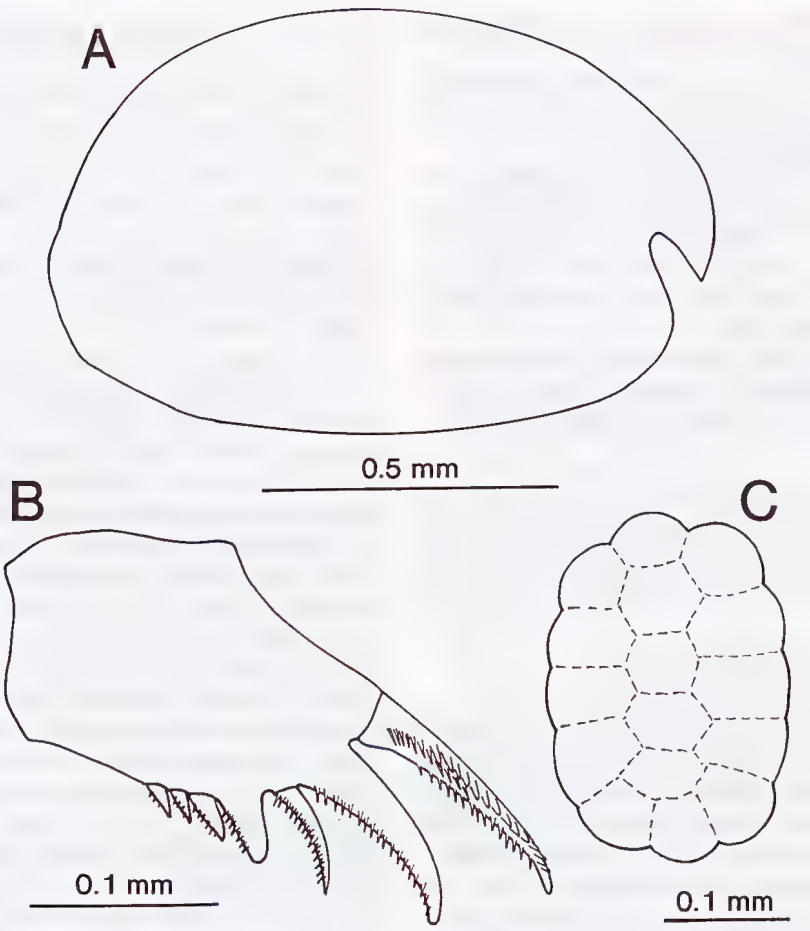

Fig. 8. *Lowrya kornickeri* juvenile (A-1) female (AM P45464). **A**, right carapace valve, lateral view. **B**, left furcal lamella, medial view (right lamella with 8 claws). **C**, left lateral (compound) eye, lateral view (dorsal above).

claw 4 exceptionally broad; claw 5 short and broad; anterior claws short and broad; claws generally increasing in size posteriorly; claws generally slightly curved; all claws with spinules; distal medial robust setules of most posterior claw broad; lamellae with concave posterior part of ventral margin, leading to an anterior ventral hump; left lamella bare, right lamella with medial long thin setae near distal ventral margin.

ANTERIOR OF BODY (Fig. 6E). *Bellonci organ*: (non-extended) is trapezoid (terminal margin longer than basal margin); length (non-extended) = 0.03 mm; width greater than length; tip (extended) bluntly rounded; without pigment.

Eyes: *medial eye* (Fig. 6E) large, length = 0.06 mm; pigmented. *Lateral eye* (Fig. 6E): very large, length = 0.27 mm; about 10 times size of medial eye; broadest dorsally; with at least 16 ommatidia (7 large, of approximately equal size; 9 small, of approximately equal size), largest ommatidia located dorsally; ommatidia light amber in transmitted light, matrix between ommatidia maroon in transmitted light.

Upper lip (Fig. 6E): pigmented. *Anterior*: single undivided process directed anteroventrally; ventral field of process pear-shaped, with about 16 large valves, arranged in about 3–5 anterior-posterior rows on a single plane; anterior process bare. *Posterior*: with very fine setae posteriorly. *Tusks*: short, consistently medium width; each with 2 valves, valves medium sized, forming a step-like profile of posterior tusk margin; tusks without setae or spines; spurs on tusks absent.

Frontal knob (Fig. 6E): large, rounded, width less than length; no projections ventral to frontal knob.

POSTERIOR OF BODY. *Dorsal folds*: absent. *Y-sclerite*: ventral branch <50% length of dorsal branch.

Description of juvenile (A-1) female characters.

Most characters common to both sexes have been omitted from the following description.

CARAPACE (Fig. 8A). Length = 1.14 mm, height = 0.70 mm; length/height = 1.63.

FIRST ANTENNA. Without "suckers" and basal setules of b- and c-setae; all halophores without spinules.

MANDIBLE. All setae generally with less spinules than male. *Second endopodial article*: dorsal margin with 7 bare setae; 1 a-, 1 b-, 2 shorter-, 1 c-, 2 d-setae (no setae distal to d-setae). *Third endopodial article*: c-seta of left limb curves in opposite direction to claws and b- and d-setae

(probable artifact of slide preparation); c-seta of right limb similar to that of the male.

SIXTH LIMB. *Terminal article*: row of 4 anteroventral setae.

SEVENTH LIMB. Total of 8 setae. *Comb side*: without non-terminal setae; 3 terminal setae.

FURCA (Fig. 8B). Left lamella with 7 claws, right lamella with 8 claws; claws 2 and 4 proximally broader than in male; large medial robust setae of claw 1 (most posterior claw) present along almost complete length of claw; lamellae irregularly shaped, with very prominent hump midway along ventral margin.

ANTERIOR OF BODY. *Lateral eye* (Fig. 8C): large, length = 0.27 mm; broadest centrally (dorsal side similar size to ventral side); with at least 16 equally sized ommatidia.

Etymology. This species is named in honour of Louis S. Kornicker, myodocopid ostracod expert, who has described a large proportion of the known myodocopines, and taught the author important techniques for working with ostracods.

Discussion

Species of *Lowrya* are scavengers. The well-developed "armature" of their fourth and fifth limbs (many terminal setae with large spinules or denticles) and large spinules on most mandibular claws are probably useful adaptations to feeding since these parts are all used in the scavenging feeding process. However, cypridinids known not to scavenge also possess such armature, to some extent. Also the broad fourth claw of the furcae of *Lowrya* may be an adaptation to scavenging because the furca plays an important role in tearing into animal carcasses (Parker, 1997b). Other scavenging cypridinids do not possess such a broad fourth claw of the furca.

Lowryi taiti n.sp. and *L. kornickeri* are relatively easy to identify under a dissecting microscope by non-ostracod specialists, without making dissections. They are relatively small cypridinids, all with a similar, rectangular oval, carapace shape, with a red colouration of a section of the rostrum visible from certain directions (present in preserved specimens). This red colouration is a structural colour (no pigments involved) and is therefore caused by the physical nature of the sclerotized area of the rostrum. The precise mechanism behind this reflection can only be determined using transmission electron microscopy. It is unusual because previously known forms of sclerotization are either colourless, a deep amber or brown/black (due to melanin) in crustaceans (Stevenson, 1985). The red colour in *Lowrya*, however, is rather weak and may not be functional. Red light may not be present at the depths where *Lowrya taiti* n.sp. exist (Jerlov, 1976). This colour is probably incidental to the strong lateral processes of the rostrum, which provide a cover for the second antennae when protruded through the incisure. This may provide protection from sediment during digging, where the second antennae plays a major role (see Vannier & Abe, 1993).

The distribution of small "suckers" on the non-basal setules of the b- and c-setae of the adult male first antennae of *Lowrya kornickeri* and *L. taiti* indicates that they belong in the *Cypridina* group within the Cypridinini (definitions from Kornicker 1975, 1983). The large basal "suckers" of the c-setae of the male first antennae of *Lowrya kornickeri* and *L. taiti* (a character shared only with *Sheina orri*), and the intriguing cup-shaped sections from which they arise, justify a functional morphology study of these, and all other male first antennal "suckers" within the Cypridinidae. These "suckers" are supposedly suctorial organs used by the adult male to grasp the female during copulation, as observed in a contentious study of *Vargula hilgendorfii* (Müller, 1890) (Okado & Kato, 1949). However, from video recordings of a species of *Skogsbergia*, a cypridinid with male first antennal "suckers", during mating, it was observed that these "suckers", or any part of the male first antenna, did not make contact with the female (Parker, 1997a). Therefore, the possibility that these "suckers" have a sensory function (Kornicker, 1983) should be investigated. The cup-shaped basal sections, and the bulbous proximal parts, of the basal setules of the c- and b-setae of the male first antennae of *Lowrya kornickeri* and *L. taiti* provide evidence for a functional mechanism for the whole "sucker" system which is more complex than one required for a "simple" suctorial organ. Additionally, the large "sucker" of the c-seta of the male first antenna of *Lowrya kornickeri*, at least, might be somewhat restricted by its position (Fig. 6J) to function as a suctorial organ. In living *Azygocypridina lowryi* Kornicker, 1985, in a large petri dish full of water, the largest angular movement of first antennal setae is only about 15° (Parker, 1998). It can be noted that the large "suckers" (at least) bear a close resemblance to the calceoli of certain amphipods; the calceolus is a presumed sensory receptor (Lincoln & Hurley, 1981). Lincoln (1985) suggests, with evidence, that the calceoli may function as phonoreceptors, sensitive to water borne pressure waves.

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A Third Species of *Aatolana* Bruce, 1993 (Crustacea: Isopoda: Cirolanidae)

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ABSTRACT. A third species of *Aatolana* is described from material collected in baited traps deployed off the north east coast of Australia. This species can be distinguished from the other species in the genus principally by the morphology of the frontal lamina, coxa 7 and uropods, length of the antennae, and setation of pereopod 7 and the pleotelson. A key to the three species in the genus, an emended generic diagnosis and a discussion of the systematic position of the genus are also presented based on the examination of new material. This examination shows that, of the apomorphies which have been suggested to characterise species of *Aatolana*, only the enlarged and setose epimera of pleonite 3 can be recognised as a putative unique synapomorphy that unambiguously defines the genus. The morphology of the frontal lamina of the new species of *Aatolana* described here is also recognised as an additional character shared with species of *Booralana* Bruce, 1986, further suggesting a close relationship between species in these two genera.

KEABLE, S.J., 1998. A third species of *Aatolana* Bruce, 1993 (Crustacea: Isopoda: Cirolanidae). Records of the Australian Museum 50(1): 19–26.

Species in the family Cirolanidae are among the most commonly encountered isopod crustaceans in shallow marine environments (Bruce, 1993a). Many cirolanid isopods are scavengers, feeding on the carcasses of animals they have not captured and killed themselves, and cause losses to fisheries by feeding on baits or catches (Stepien & Brusca, 1985; Bruce, 1986; Berrow, 1994; Mizzan, 1995). The importance of scavenging cirolanid isopods to marine food chains has been suggested by Keable (1995) who also described the design of a baited trap which can be used to readily sample these and other scavengers.

Recent revisions of the Cirolanidae include those of Bruce (1981a, 1986) and Brusca *et al.* (1995). Bruce (1981a: 961, 1986: 140, 223) considered that *Cirolana schioedtei* Miers, 1884 could not be readily placed in *Cirolana* because this species possesses several characters that are not shared with other species placed in this genus. Recognition of a second species similar to *C. schioedtei* provided Bruce (1993b) with a foundation to establish the genus *Aatolana* to accommodate these two species. Further records of these species were provided by Keable (1997). Keable (1997) also designated a lectotype for *A. schioedtei* and suggested that previous records of this species need to be revised because they may include records of undescribed species of *Aatolana*. Examination of material collected with baited traps during the SEAS (Scavengers of East Australian Seas) project (J.K. Lowry, unpublished data) revealed the existence of a third species of *Aatolana* which is described here. This allows some further information to be added to the generic diagnosis and discussion of relationships to other genera provided by Bruce (1993b) for *Aatolana*.

Methods

The anatomical terminology and the conventions regarding orientation of appendages applied here follows that used by Bruce (1986, 1993b) and adopted by Keable (1996a).

Examination and illustration of specimens follows the methods outlined by Keable (1997).

The following abbreviations are used in the text and plates: **AM**—the Australian Museum, Sydney; **BMNH**—the Natural History Museum, London; **USNM**—National Museum of National History, Smithsonian Institution, Washington, D.C.; **ZMUC**—Zoologisk Museum, University of Copenhagen, Copenhagen; n—number of specimens; **CE**—cephalon; **A1**—antennule; **A2**—antenna; **CL**—clypeal region; **FL**—frontal lamina; **MD**—mandible; **MP**—maxilliped; **MX1**—maxillule; **MX2**—maxilla; **PE**—penes; **PN**—pleon; **P1–7**—pereopods 1–7; **U**—uropod; **PL1–5**—pleopods 1–5; **PT**—pleotelson.

Taxonomy

Aatolana Bruce

Aatolana Bruce, 1993b: 2.–Brusca *et al.*, 1995: 96.

Type species: *Aatolana rapax* Bruce, 1993b (by original designation).

Diagnosis: *Frontal lamina*: short, length approximately 1.3–2.5 × basal width; anterior margin convex with a dorsally deflected apical point, or with an excavate extension; ventral surface flat, or with the posterior section projecting. *Clypeus*: ventral surface not projecting relative to frontal lamina. *Antenna*: peduncular articles 1 and 2 shortest, subequal; peduncular article 4 longer than article 3; peduncular article 5 longer than article 4 and all other articles. *Pereon* and *pleon*: dorsal surfaces without setae, tubercles, processes or furrows. *Pleonite 3*: epimera broader than that of other pleonites, with lateral row of slender setae; dorsal and ventral posterolateral margins convex, converging smoothly to a point, posteroventral excision absent; enclosing but not covering epimera of pleonite 4; extending to or beyond posterior of pleonite 5. *Pleonite 5*: posterolateral margins encompassed by pleonite 4. *Pereopods 1–7*: dactylus with secondary unguis present or absent; secondary unguis not large and strongly sclerotized when present. *Pereopod 1*: merus anterodistal angle not produced to posterodistal extent of carpus or beyond. *Pereopod 7*: basis, ischium and merus with or without plumose setae. *Penes*: present; short, approximately 2 × width; forming well separated flattened lobes. *Pleopod 2 appendix masculina*: arising basally; longer than endopod in fully developed specimens; slender. *Pleopods 1–5*: endopod plumose setae present across distal margins of pleopods 1–4 and absent on pleopod 5.

Additional characters: *Body*: narrow, length 2.0–3.5 × greatest width; lateral margins sub-parallel in dorsal view. *Cephalon*: broad, width greater than 60% of pereonite 1; moderately enclosed by pereonite 1; without tubercles or processes; anterior margin with medial indentation, not extending to cover proximal articles of antennule; rostrum not prominent. *Eyes*: well developed, ommatidia clearly defined, pigmented; elongate, length approximately 3 × width; not divided by unfaceted band. *Frontal lamina*: visible in dorsal view; forming an angle of 90° or of less than 45° with clypeus; not fused to cephalon. *Antennule*: colinear, peduncular article 2 not at right angles to article 1; much shorter than antenna, just reaching pereonite 1. Peduncular articles 1–3 not fused; article 3 well developed, longer than articles 1–2, or subequal to article 1 with article 2 shortest. Accessory flagellum absent. Primary flagellum longer than peduncle; callynophore absent. *Antenna*: not sexually dimorphic. Peduncle comprised of 5 articles. Flagellum much longer than peduncle.

Mandible: molar well developed; medial surface with slender setae; marginal robust setae present, numerous. Incisor broad, wider than narrowest part of mandible; serrate; not quadridentate on left mandible. Lacinia mobilis absent or present on left mandible as a triangular sclerotized process embedded between the setal row and the incisor. Setal row present, well developed, with numerous robust setae; intermediate slender setae absent. Palp 3-articulate; inserted adjacent to molar; article 3 distally narrow. *Maxilla*: lateral lobe and middle lobe subequal; medial lobe short and broad; lateral, middle and medial lobes with numerous setae. *Maxilliped*: palp medial margin with slender setae on more than half the length of articles 2–5; lateral margin with slender or plumose setae along most of the length of articles 2–5; article 3 with distal margin width greater than proximal margin of article 4; article 4 with distal margin width greater than proximal margin of article 5. Endite with coupling hooks.

Pereon: pereonite 1 distinctly longer than pereonite 2. *Coxae*: not forming sternal plates.

Pleon: not sexually dimorphic; five unfused segments present, all equally visible along dorsal margin, or pleonite 1 partially or completely concealed by pereonite 7, in dorsal view all appearing broader than pleotelson.

Pleotelson: dorsal surface smooth with anterodorsal depression, tubercles, pits and ridges absent, setae present or absent; margins convex, meeting at an acute apex; marginal robust setae present; marginal plumose setae present, restricted to posterolateral margins, abundant; marginal teeth-like serrations absent.

Pereopods 1–3: ischium anterodistal angle produced subequally. Merus anterodistal angle more produced on pereopods 2 and 3. Dactylus not longer than propodus. *Pereopod 7*: coxa not extending beyond posterior of pleon. Basis not noticeably broader in distal half compared to proximal half; anterior margin with long plumose or slender setae along entire length (using the conventions for pereopod orientation outlined by Bruce (1993b), not the posterior margin as he states); medial carina with plumose or slender setae along most of length of article, or slender setae only distally; posterodistal angle without long plumose setae. Ischium anterior margin with plumose and slender setae present or absent, setae abundant and occurring along entire length when present; posterior margin with plumose and slender setae absent. Merus anterior margin with slender setae absent, plumose setae

present or absent; posterior margin with plumose and slender setae absent.

Pleopods: peduncle respiratory branchiae absent; accessory lobe well developed, with complex folding. *Pleopods 1–4*: exopods with slender accessory lamella at posterior proximolateral angle; endopods with elongate laterally curving lobe arising from proximomedial angle. *Pleopod 1*: not operculate to posterior pleopods; peduncle length shorter than breadth; exopod and endopod narrow, length greater than 2 × width; exopod medial margin convex, narrow at apex, lateral margin relatively straight; endopod width greater than 0.5 × width of exopod.

Uropods: inserted ventrolaterally on pleotelson; extending posteriorly beyond pleotelson. Peduncle strongly produced along medial margin of endopod. Endopod and exopod margins with robust setae; plumose setae present on most of margin length; apices sub-bifid, without robust setae. Endopod lateral margin sinuate, straight or slightly convex (not concave); without prominent lateral excision; without distinct pit. Exopod dorsoventrally flattened, not extending posteriorly beyond endopod.

Remarks. The diagnosis and description of *Aatolana* provided by Bruce (1993b) is emended here based on the material of *Aatolana* examined in this study and in that of Keable (1997). Particularly important changes to the original diagnosis of *Aatolana* include: the recognition of a small secondary unguis on the dactylus of pereopods 1–7 in the species described here; variation in the form of the frontal lamina; and variation in the setation of pereopod 7.

Three unique apomorphies characterising species of *Aatolana* were recognised by Bruce (1993b): the prominent, posteriorly acute epimera of pleonite 3; the complex refolded lobe on the lateral margin of the peduncle of pleopods 1–5; and the structure of the frontal lamina. Of these suggested apomorphies, only the enlarged epimera of pleonite 3 (which is made additionally distinctive by having a row of slender setae along the medial longitudinal carina of the lateral surface) is shared exclusively between species of *Aatolana* and remains as a putative unique synapomorphy of these species that unambiguously defines the genus. Examination of all three species of *Aatolana* and also the figures of *A. rapax* Bruce, 1993b, shows that the refolding of the lobe on the lateral margin of the pleopod peduncle is poorly developed on pleopod 1 but characteristic of pleopods 2–5 (Keable, 1996b). On these pleopods the lobe extends distally on the peduncles (see Fig. 2). Furthermore, examination of specimens of species of *Bathynomus* A. Milne Edwards, 1879, *Booralana* Bruce, 1986 and an undescribed taxon similar to *Dolicholana elongata* (H. Milne Edwards, 1840) show that they have a comparable lobe on the lateral margin of the peduncle of the pleopods (Keable, 1996b). Additionally, the structure of the frontal lamina cannot be recognised as a unique synapomorphy shared by species of *Aatolana* because this character varies considerably among the three species now placed in this genus and can actually be used to discriminate these species (Keable, 1997; this study). However, the variation in structure of the frontal lamina found in these species is relatively simple and it may be possible to hypothesize a transformation series for this character when the phylogeny of the Cirolanidae is better understood.

Bruce (1993b) suggested that species of *Aatolana* were similar only to species of *Booralana*, with which they share comparable elongate eyes, prominent flattened penes, a medially indented cephalon and prominent epimera on pleonite 3. Bruce (1993b) further noted that the structure of the frontal lamina differed between species placed in these two genera. However, the frontal lamina of species of *Booralana* has been described as being formed from two parts, an anterior half and a posteroventral section which projects (Bruce, 1986; Camp & Heard, 1988). This description matches that of the frontal lamina of the species of *Aatolana* described here. Furthermore, an additional character shared between species placed in these two genera, which has not been remarked upon previously, is the slender accessory lamella at the posterior proximolateral angle of the exopod of pleopods 1–4 which has been described in species of *Aatolana* (Holdich *et al.* 1981; Bruce, 1986, 1993b; this study). The shape and position of this lamella indicates its homology with the upturned lobe found in this location in species of *Booralana* (see Camp & Heard, 1988, figs 4A–E; Keable, 1996b). While *Aatolana* has not been placed in a subfamily these additional characters further suggest a close relationship with *Booralana*. *Booralana* has also been linked with *Bathynomus*, *Parabathynomus* Barnard, 1924 and *Cirolana quadripustulata* Hurley, 1957 (Bruce, 1981a, b, 1986; Botosaneanu *et al.*, 1986; Wägele, 1989). *Bathynomus* and *Parabathynomus* have been placed in the subfamily Cirolaninae Dana, 1852 while *C. quadripustulata* remains *incertae sedis*. However, according to Bruce (1986: 223) *C. quadripustulata* also shares characters found in *Natatolana* Bruce, 1981a which is placed in the Conilerinae Kensley & Schotte, 1989.

An additional noteworthy character found in species of *Aatolana*, which has not been remarked upon previously, is the presence of a large, triangular, highly sclerotized structure imbedded in the body of the left mandible between the setal row and the incisor (Fig. 1). This structure occurs in *A. rapax* and the species described here but not *A. schioedtei*. A similar large triangular structure is found partially fused to the distal side of the setal row on the left mandible of species of *Bathynomus* (see illustrations of *B. giganteus* A. Milne Edwards, 1879 by A. Milne Edwards & Bouvier (1902, plate 4) and also *B. immanis* Bruce, 1986 and *B. pelor* Bruce, 1986 by Bruce (1986, figs 90F, 91F); Keable (1996b, plate 2.2.2). This structure appears to be absent in many other genera of the Cirolanidae (Keable, 1996b). The function and phylogenetic significance of this structure is unknown. Although Brusca *et al.* (1995) concluded that a lacinia mobilis is absent in the Cirolanidae, the morphology and position of this structure in *Bathynomus* suggest it is homologous to the lacinia mobilis of other peracaridan crustaceans. It also appears to play a similar role as a guiding and locking mechanism for the mandible (Dahl & Hessler, 1982). This structure cannot act in the same way as a lacinia mobilis in species of *Aatolana* because it is embedded in the mandible surface. However, this may represent a transition from the condition found in *Bathynomus*.

Key to species of *Aatolana*

1 Frontal lamina, anterior margin forming an excavate process; coxa 7, posterior margin concave; basis of pereopod 7, anterior margin with plumose setae; pleotelson, dorsal surface with setae; uropod rami, lateral margins sinuate ..... *A. schioedtei*

—— Frontal lamina, anterior margin convex with a small process protruding between the antennal bases, or acute and deflected dorsally from a rounded posteroventral projection; coxa 7, posterior margin straight or convex; basis of pereopod 7, anterior margin with setae which lack setules; pleotelson, dorsal surface without setae; uropod rami, lateral margins straight or slightly convex 2

2 Frontal lamina, anterior margin convex with a small process protruding between the antennal bases; antenna extending to the posterior of pereonite 5 ..... *A. rapax*

—— Frontal lamina, anterior margin acute and deflected dorsally from a rounded posteroventral projection; antenna extending to the posterior of pereonite 4 ..... *A. springthorpei* n.sp.

Aatolana springthorpei n.sp.

Figs 1–2

Type material: HOLOTYPE: ♂, 48 mm, AM P47650. PARATYPES: ♂, AM P47651; ♂, ZMUC CRU2395; ♂, USNM 282732; ♂, BMNH 1997.1752.

Type locality: off East Fitzroy Reef, Queensland, Australia, 23°32.16'S 152°17.98'E, baited trap, 17.8°C, 203 m, J.K. Lowry, P. Freewater & R.T. Springthorpe on MV Reefknot, 16–17 June 1993, SEAS QLD-958.

Additional material examined: 2 ♂♂, 2 ♀♀ (1 damaged), AM P47652, east of Coffs Harbour, New South Wales, Australia, 30°14.63'S 153°27.68'E, baited trap, 199 m, P.B. Berents, R.T. Springthorpe & W. Vader 12–13 Aug. 1993, SEAS NSW-883.

Diagnosis: *Frontal lamina*: with a rounded posteroventral projection. *Antenna*: 0.4 × as long as body; when extended against the body reaching to posterior of pereonite 4. *Pereopod 7*: basis anterior margin with long slender setae present along entire length. *Uropods*: endopod lateral margin slightly convex; exopod lateral margin convex.

Material described: Holotype.

Description: Male. *Overall body form*: large; 48 mm long; narrow, length approximately 3.3 × width. Colour cream in alcohol. Chromatophores absent.

Cephalon: anterior margin recessed with a small ventrally directed rostrum below margin; submarginal cephalic furrow well developed, runs entire length of anterior margin. *Eyes*: with 20 ommatidia in horizontal diameter; with 9 ommatidia in vertical diameter; rectangular (bisected by anterior margin); black-red/brown in alcohol. *Interocular furrow*: moderately developed, distinct but not extending across the cephalon. *Frontal lamina*: length approximately 1.3 × basal width; pentagonal in ventral view, with a rounded posteroventral projection. *Clypeus*: triangular; not sculpted. *Labrum*: flat; narrower than clypeus. *Antennule*: peduncular article 1 longer than article 2; article 2 with 1 slender seta on posterior margin, 2 penicillate setae at posterodistal angle and 2 penicillate setae on anterior margin; article 3 long, larger than article 1 or 2 but shorter than their combined lengths. Flagellum 32-articulate; aesthetascs present. *Antenna*: of medium length, 0.4 × as long as body; when extended against the body reaching to posterior of pereonite 4. Peduncular article 4 with several slender setae on distal margin; article 5 with several slender and penicillate setae along distal margin. Flagellum 49-articulate.

Mandible: molar medial surface smooth, short fine slender setae restricted to posterior margin, long slender setae along anterior margin; incisor tridentate, with strongly developed posterior tooth; palp article 2 approximately 2 × the length of article 3, provided with numerous slender setae distally and minutely biserrate slender setae proximally; lacinia mobilis-like structure present on left mandible only, forming a dark brown highly sclerotized triangular structure, embedded in the body of the mandible separate to the raised setal row; setal row with 19 robust setae. *Maxillule*: medial lobe with 3 large and 1 smaller robust pappose setae, lateral margin with protuberance well developed; lateral lobe with 13 robust setae on distal surface (2 of which are slender). *Maxilla*: lateral lobe slender, with 10 slender setae; medial lobe with 22 slender and 11 plumose setae; middle lobe with 18 slender setae. *Maxilliped*: palp moderately setose; articles

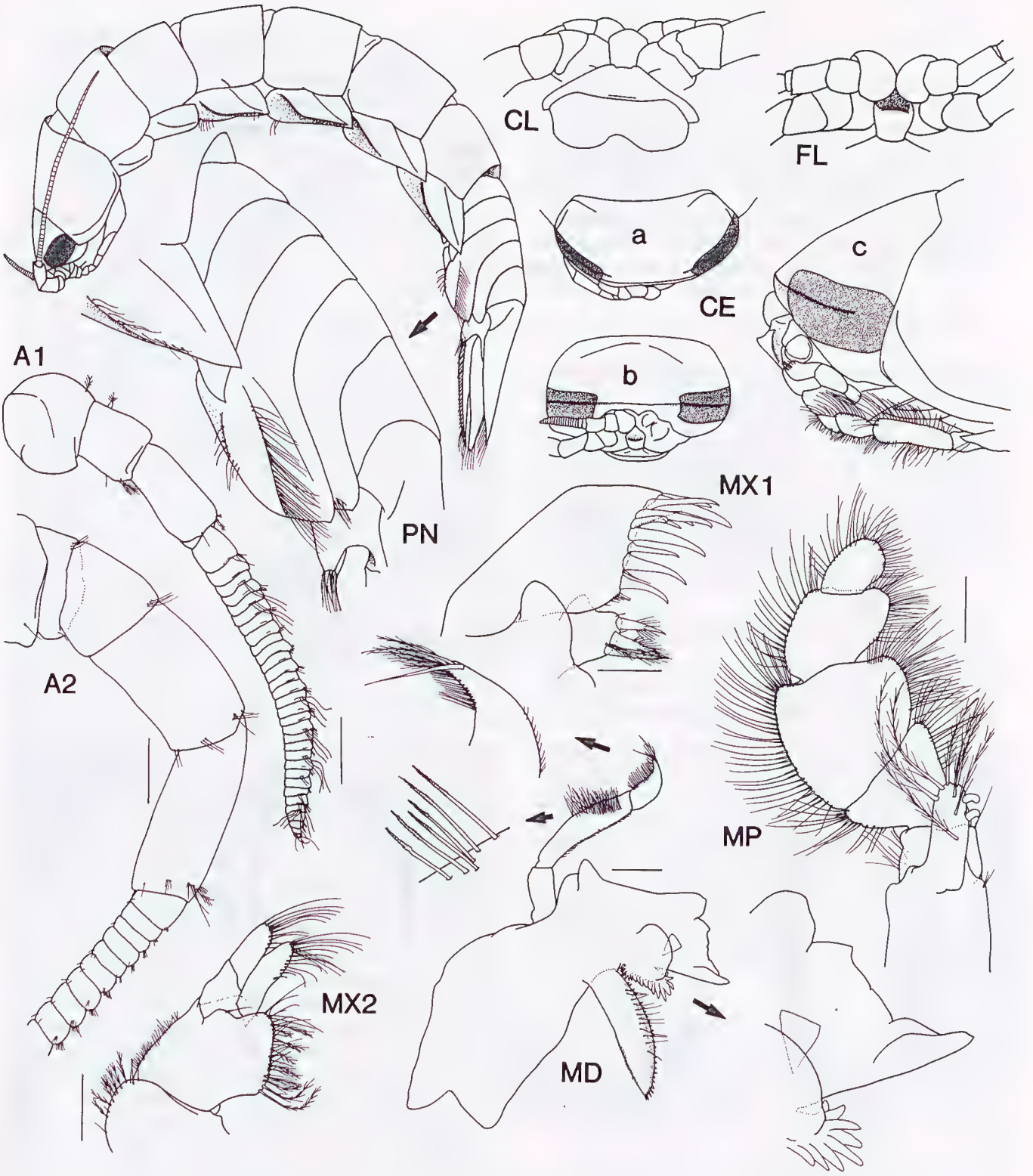

Fig. 1. *Aatolana springthorpei*, holotype. CE a, b and c are dorsal, anterior and lateral views of cephalon, respectively. Scales = 0.5 mm.

not fused; article 3 length subequal to breadth; article 4 length less than breadth; article 5 length greater than breadth, with serrate setae present; lateral margin with slender setae along most of the length of articles 2–5, plumose setae absent. Endite with 2 coupling hooks, and 8 plumose setae.

Pereon: ornamentation consists of 1 strongly developed furrow on lateral margin of pereonite 1 and 1 short, medial furrow on lateral margins of pleonites 4–7; pereonite 1 longest, 4–6 subequal and longer than 2–3 and 7 which are subequal. *Coxae*: furrows strongly developed, on all coxae, anteroventral corners of coxae 4–7 sloping

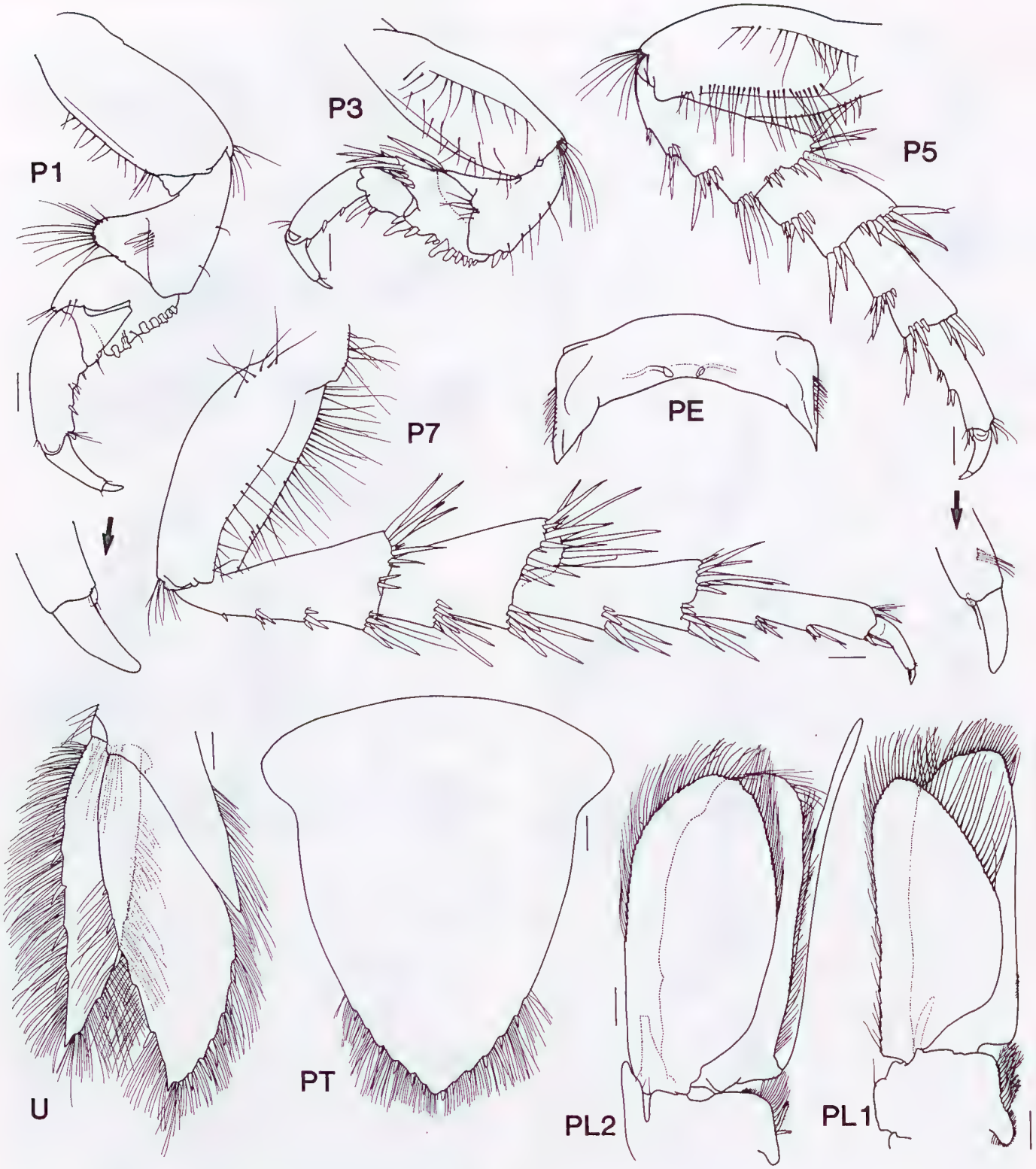

Fig. 2. *Aatolana springthorpei*, holotype. Scales = 0.5 mm.

ventromedially. Coxal points variously developed, pereonite 1 and coxae 2–3 with rounded posteroventral corners, coxae 4–7 with increasingly produced, broad, acute posteroventral corners.

Pleonites: 5 present, all equally visible along dorsal margin; ornamentation consists of 2 strongly developed furrows on lateral margin of pleonite 2 and 3 on lateral margin of pleonite 3. *Pleonite 1*: posterolateral margins produced, dorsal margin much more produced than ventral margin. *Pleonite 2*: dorsal posterolateral margin clearly projecting posterior to ventral posterolateral margin. *Pleonite 4*: posterolateral margins extending subequal to pleonite 3; posterodorsal margin strongly concave proximal to meeting posteroventral margin at apex; apex slightly rounded.

Pleotelson: narrow, length 1.1 × basal width; dorsal surface smooth, setae, ornamentation and sculpting absent; anterolateral margins convex; posterolateral margins convex, meeting smoothly to a point; robust setae present, 12 altogether, 6 on each posterolateral margin; marginal plumose setae present, restricted to posterolateral margins, abundant.

Pereopods 1–7: dactylus with a distinct secondary unguis. *Pereopod 1*: basis with slender setae on anterior margin; posterodistal angle with a group of slender setae. Ischium anterodistal angle without robust setae, 1 row of slender setae along margin; posterior margin without robust setae, slender setae present, sparse. Merus anterodistal angle without robust setae, but with approximately 4 slender setae; anterior margin without robust setae; posterior margin bisinuate, with 7 robust setae and approximately 3 slender setae. Carpus without robust setae, slender setae present. Propodus with 3 robust setae on palm, with 1 robust seta opposing dactylus; marginal slender setae present; anterodistal angle with sparse slender setae. Dactylus long, subequal in length to propodus. *Pereopod 2*: ischium anterodistal angle with 1 robust seta; posterior margin with 2 robust setae. Merus anterodistal angle with 5 robust setae; posterior margin with 10 robust setae. Carpus with 2 robust setae. Propodus with 2 robust setae on palm; 1 robust seta opposing dactylus. *Pereopod 3*: ischium posterior margin with 2 robust setae. Merus anterodistal angle with 8 robust setae; posterior margin with 11 robust setae. Carpus with 2 robust setae. Propodus with 2 robust setae on palm; 1 robust seta opposing dactylus. *Pereopods 4–6*: becoming progressively longer. *Pereopod 4*: similar to pereopods 5–7. *Pereopods 5–7*: relative morphology similar, width and setation of articles not varying markedly. *Pereopod 6*: basis broader than that of pereopod 7; propodus shorter than that of pereopod 7. *Pereopod 7*: basis narrow, width 0.4 × length; anterior margin straight, long slender setae present along entire length; medial carina with slender setae present; posterior margin convex, with slender setae present on proximal quarter; posterodistal angle with slender setae present. Ischium length greater than width; anterior margin without setae; anterodistal angle with 7 robust setae, non-robust setae absent; posterior margin with 8 robust setae, non-robust setae absent; posterodistal angle with 5 robust setae, slender setae present. Merus length greater than width; anterior margin without setae; anterodistal angle with 16 robust setae, 1 slender seta present; posterior margin with 6 robust setae; posterodistal angle with 7 robust setae, non-robust setae absent. Carpus anterior margin without setae; anterodistal angle with 9 robust setae, slender setae present; posterior margin with 6 robust setae, 1 slender seta present; posterodistal angle with 7 robust setae, non-robust setae absent. Propodus subequal to carpus; anterior margin without setae; anterodistal angle with 1 robust seta, slender setae present; posterior margin with 8 robust setae, non-robust setae absent; posterodistal angle with 2 robust setae, non-robust setae absent.

Pleopod 2 appendix masculina: 1.3 × length of endopod; margins bent slightly medially, somewhat broader proximally but otherwise approximately parallel along entire length; slender; apex not at angle to margins, bluntly rounded. *Pleopods 1–5*: exopod suture strongly developed on pleopods 3–5 only.

Uropods: peduncle ventrolateral angle with 2 robust setae, and 10 plumose setae. Endopod lanceolate; medial margin convex, with 6 robust setae, plumose setae present, along entire length; lateral margin slightly convex, with 6 robust setae, plumose setae present, on distal two-thirds. Exopod slightly shorter than endopod, 0.88 × the length of the endopod; lanceolate; medial margin convex, with 4 robust setae, plumose setae present, on distal three-quarters; lateral margin convex, with 6 robust setae, plumose setae present, along entire length.

Sexual dimorphism: Female similar to male.

Variation: Pleotelson and uropod robust setal counts from margins (n = 4 but damaged specimens omitted; paratypes): Pleotelson: 7:6 100% (3 specimens damaged); endopod (medial): 7–50%, 6–25%; (lateral): 6–25%, 5–50%; exopod (medial): 4–50%, 3–25%; (lateral): 9–25%, 8–25%, 6–25%, 5–25%. AM P47652 (n = 4—but damaged specimens omitted): Pleotelson: 7:8–25%, 7:7–25%, 6:6–25%; endopod (medial): 10–25%, 7–50%, 6–25%; (lateral): 6–25%, 5–50%; exopod (medial): 5–25%, 4–75%; (lateral): 9–50%, 8–50%.

Size range: Adults to approximately 50 mm.

Etymology: This species is named after Mr R. Springthorpe who assisted in collecting the type specimens, in recognition of the help he has given me with this and other projects.

Remarks. *Aatolana springthorpei* is most similar to *A. rapax* but can be distinguished by the posteroventrally projecting frontal lamina and shorter antennae (extending to the posterior of pereonite 5 in *A. rapax*). *Aatolana schioedtei* is also similar. However, in *A. schioedtei* the structure of the frontal lamina differs, the posterior margin of coxa 7 is distinctly concave, the lateral margins of the uropod rami are strongly sinuate (especially the exopod), pereopod 7 has a greater number of distinctly plumose setae on the margins of the basis, ischium and merus, and the pleotelson of adults has fine setae covering much of the dorsal surface.

Parker (1995) reported that iridescence may be displayed by light reflected from diffraction gratings occurring on the aesthetascs of the antennule of *Aatolana rapax*. This was based on observations of the material examined by Keable (1997). Similar iridescence is also encountered in a variety of other cirolanid isopods, such as *A. springthorpei*, *A. schioedtei*, *Bathynomus* spp., *Booralana* spp., *Cirolana* spp., *Plakolana* spp. and an undescribed taxon similar to *Dolicholana elongata*, but has not been found in any species of *Natatolana* (personal observation).

Distribution: east coast of Australia—off northern Queensland and New South Wales. In depths of approximately 200 m.

Ecology: *Aatolana springthorpei* is a scavenger as are other members of the genus (Bruce, 1993b; Keable, 1997).

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Siphonoecetinae (Crustacea: Amphipoda: Ischyroceridae) 7: Australian Concholestids, *Ambicholestes* n.gen., with a Description of Six New Species, and a New, Restricted Diagnosis for *Caribboecetes* Just, 1983

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ABSTRACT. A new genus, *Ambicholestes*, of concholestid Siphonoecetinae is described. *Caribboecetes* Just, 1983 is re-diagnosed to encompass *C. barbadensis* Just, 1983 (type species), *C. jenikarpae* Just, 1984a, *C. intermedius* Just, 1984a and, tentatively, *C. pterycornis* Just, 1984a only. *Caribboecetes crassicornis* Just, 1984a, *C. magellani* Just, 1984a and *C. squamiferus* Just, 1984a are transferred to *Ambicholestes*, together with six new species from Australia: *A. cygnatratus, A. poorei, A. trilobatus, A. berentsae, A. thetis*, and *A. minutus*. The three last mentioned species are placed in a new subgenus, *Austrolestes*. The main character distinguishing *Ambicholestes* s.l. from *Caribboecetes* is the presence in the former of unique, complexly lobate inner lobes of the lower lip.

A possible stridulation organ involving coxal plate 2 and pereopod 2 is described for three species of *Ambicholestes*. A key to Australian *Ambicholestes* is provided. *Ambicholestes squamiferus* is recorded from Guam.

JUST, J., 1998. Siphonoecetinae (Crustacea: Amphipoda: Ischyroceridae) 7: Australian concholestids, *Ambicholestes* n.gen., with a description of six new species, and a new, restricted diagnosis for *Caribboecetes* Just, 1983. *Records of the Australian Museum* 50(1): 27–54.

Siphonoecetine amphipods are small (2–15 mm) marine crustaceans found in a variety of sheltered sandy or muddy places from the low water mark to several hundred metres depth, occasionally in very dense aggregations. Individual amphipods occupy tiny empty snail shells or worm tubes, which they carry around in a crawling or jumping manner. Siphonoecetines have been found around most continents except Antarctica and the North Polar Ocean, but many species remain to be described, not the least around Australia and south-east Asia. A brief overview of siphonoecetine classification, distribution and biology is presented by Just (1988).

This study is the second in a planned series describing the rich Australian fauna of Siphonoecetinae. *Australoecetes* Just, 1983 was dealt with in detail by Just (1985). Preliminary results from field work and museum studies in Australia in 1984 were used in phylogenetic, biogeographic, and biological contexts by Just (1988). In

the latter study the Siphonoecetinae was informally divided into concholestids and siphonoecetids. The former group is characterised by: coxal plates 3–4 having the distal margin dentate with thick, squamose setae; article 4 in pereopods 3–4 being anterolobate only; the dactylus on pereopods 5–7 having no accessory tooth; uropod 2 being absent.

In the present study, seven concholestid species, six of them new to science, are described from Australian waters (Fig. 1, distribution).

Just (1983) placed his new subfamily Siphonoecetinae in the Corophiidae, but later (Just, 1988) noted the similarity to cerapodid taxa (Ischyroceridae). Barnard & Karaman (1991) treated the subfamily as part of the Ischyroceridae complex of the Corophioidea close to *Cerapus* and allies. Lowry & Berents (1996) show that their "*Siphonoecetes* clade" (= Siphonoecetinae) and "*Cerapus* clade" (comprising five genera) are sister groups within a proposed "*Ericthonius* group" (= corophioid taxa with dorsal spines on the telson). Their study does not resolve whether or not the *Ericthonius* group belong in the Ischyroceridae. Bousfield & Hoover (1997) restrict the family Corophiidae to the newly created Corophiinae and the Siphonoecetinae. Since Bousfield and Hoover provide no supporting evidence for this sister group relationship, and they make no mention of the potential relationship between Siphonoecetinae and the ericthonid/cerapodid genera, I prefer to retain, for practical reasons, the Siphonoecetinae in the Ischyroceridae as suggested by Barnard & Karaman (1991), pending a broader based cladistic analysis of the Corophioidea.

Colour descriptions are copied from my field notes and colour transparencies of live animals. The length of animals was measured from the tip of the rostrum/front margin of the cephalon along the dorsal curvature to the apex of the telson. Names of institutions are abbreviated as follows: AM—Australian Museum, Sydney; NMV—Museum of Victoria, Melbourne; NMNH—National Museum of Natural History, Smithsonian Institution, Washington; QM—Queensland Museum, Brisbane; ZMUC—Zoological Museum, University of Copenhagen.

Review of *Caribboecetes*

Caribboecetes Just, 1983, differs from other concholestids by having a short, flattened inner ramus on uropod 1 and no ramus on uropod 3. *Concholestes* Giles, 1888 has a long and cylindrical inner ramus on uropod 1 and no ramus on uropod 3, while *Africoecetes* Just, 1983 has one ramus on uropod 3. Following the discovery of several new

Fig. 1. Distribution of species of *Ambicholestes* in Australia. Arrow points towards Chesterfield Islands in the Coral Sea.

concholestids from Australia and a re-evaluation of the *Caribboecetes* species described by Just (1983, 1984a) it has become clear that *Caribboecetes* must be divided into two groups based primarily on the structure of the lower lip and the setation on pereopod 7. *Caribboecetes barbadensis* (type-species of the genus), *C. jenikarpae*, and *C. intermedius* have the inner lobes of the lower lip simple, more or less ovoid, while *C. crassicornis, C. magellani*, and *C. squamiferus* have uniquely and complexly lobate inner lobes (Fig. 2) with a proximolateral backward curving projection on each lobe and the proximal lobe margin produced and set at an angle of up to 45 degrees with the inner lobe plane. The three last mentioned species have a midlateral, longitudinal row of setae on article 2 of pereopod 7 in addition to the normal marginal setae. The densely setose anterior lateral surfaces of coxal plate 7 and article 2 of pereopod 7 in *C. jenikarpae* are considered independently derived autapomorphisms.

On this basis a new genus, *Ambicholestes*, is established for *C. crassicornis, C. magellani, C. squamiferus* and the Australian concholestids described below. Diagnostic differences between *Caribboecetes* and *Ambicholestes* are summarised in Table 1 (p. 53).

The structure of the lower lip in *Caribboecetes pterycornis* is not known (lost during original dissection). In spite of several autapomorphic attributes, which set this species apart from other *Caribboecetes*, I tentatively retain it in that genus on account of the lack of a midlateral row of setae on article 2 of pereopod 7.

Caribboecetes Just, 1983

New restricted diagnosis. Concholestid Siphonoecetinae (*sensu* Just, 1988) with inner ramus of uropod 1 at most 1/2 length of outer ramus, flattened, with robust setae on margin. Uropod 3 without ramus. Mandibular palp 2-articulate, blunt, reaching to about apex of incisor. Inner lobes of lower lip simple. Ocular field of eye lobes not inflated. Article 2 of pereopod 7 without single midlateral row of setae. Oostegites on pereopods 2–5. Gills on pereopods 4–6.

Type species. *Caribboecetes barbadensis* Just, 1983 (original designation).

Additional species. *Caribboecetes intermedius* Just, 1984a, *C. jenikarpae* Just, 1984a, *C. pterycornis* Just, 1984a (tentatively).

Further description. Rostrum present or absent. Coxal plates 5–6 antero- as well as posterolobate (except *C. pterycornis*, posterolobate only). Upper lip with apical notch. Antenna 1 article 3 50–60% (*C. pterycornis* 70%) length of article 1, article 2 80–95% length of article 1. Antenna 2 article 4 75–90% length of article 5. Antenna 1 reaching from just beyond peduncle of antenna 2 to about tip of flagellum of antenna 2. Pereopod 1 article 6 80–90% length of article 5, without posteroapical tooth, with posteroapical robust seta and 1–2 robust setae on posterior margin; article 5 with 1 posteroapical robust seat. Pereopod 2 article 6 10–45% longer than article 5 (except *C. pterycornis*, 70%), with posteroapical triangular tooth and varying number of posterior robust setae. Pereopods 3–4 with posterior robust setae on article 5. Pereopods 5–6 with crescent of equal-sized short, robust setae on article 5. Pleopods with peduncle broader than long; rami as long as or longer than width of peduncle; inner ramus slightly longer than outer ramus.

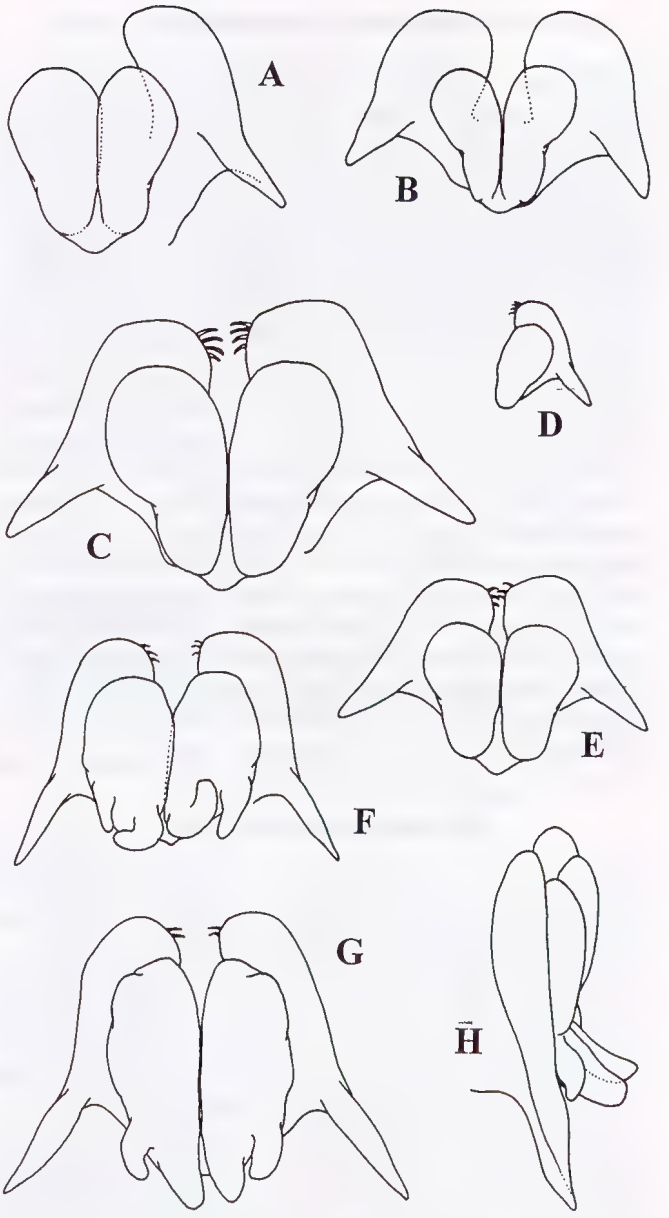

Fig. 2. Lower lip of selected concholestid Siphonoecetinae. **A**, *Concholestes omani* Just, 1987; **B**, *Africoecetes armatus* (Griffiths, 1974); **C**, *Caribboecetes barbadensis* Just, 1983; **D**, *Caribboecetes intermedius* Just, 1984; **E**, *Caribboecetes jenikarpae* Just, 1984; **F**, *Ambicholestes crassicornis* (Just, 1984, n. comb.); **G**, *Ambicholestes squamiferus* (Just, 1984, n. comb.); **H**, *Ambicholestes berentsae* n.sp., lateral view. Not to scale.

Distribution. Caribbean, Pacific Mexico; from low water mark to 54 m.

Australian Concholestids

A full cladistic analysis of the Siphonoecetinae, and the concholestid component in particular, is not feasible at the present time. Many siphonoecetines remain to be described, including groups of species exhibiting characters which will influence the outcome of such an analysis. The problem is compounded by the present uncertainties, at the outgroup level, of where the Siphonoecetinae belong in the Corophioidea, and by difficulties in delimiting families with which Siphonoecetinae are believed to be related. The proposed classification of the Australian concholestids is based on immediately obvious synapomorphies, such as a complex lower lip versus a simple one, and an elongated, 1-articulate, pointed mandibular palp versus the otherwise ubiquitous short, club shaped palp with a tiny second article (in a single known species the first article is broadly expanded). The use of subgeneric classification is a subjective convenience to keep together species sharing a major synapomorphy, e.g., the complex lower lip in *Ambicholestes*, but differing at a perceived subordinate sister group level, here *Ambicholestes* sensu stricto versus *Ambicholestes* (*Austrolestes*). This use of the subgenus category is consistent with Just (1983—*Siphonoecetes*, and 1985—*Australoecetes*).

Urosomites and the telson

In my first contribution to the taxonomy of the Siphonoecetinae (Just, 1983) an important character in the diagnosis of the new genus *Caribboecetes* was "... urosomite 3 and telson fused dorsally". This still holds good for the four species retained in that genus. For the three species of *Caribboecetes* described by Just (1984a, *C. crassicornis, C. magellani*, and *C. squamiferus*), but here transferred to *Ambicholestes* n.gen., it was noted (Just, 1984a: 38) that the urosomite-telson configuration is not intraspecifically stable (occurrence of incomplete fusion between urosomite 3 and the telson, more or less complete fusion between urosomites 1 and 2 and/or 2 and 3). The same lability is found in the Australian concholestids and will be commented upon where relevant. For that reason the urosomite-telson configuration has not been included in the diagnoses of *Caribboecetes* and the new genus group taxa below.

Stridulation organs

Three species in *Ambicholestes* s.s., viz., *A. crassicornis, A. magellani*, and *A. trilobatus* n.sp. possess what appears to be a sound producing organ. Coxal plate 2 carries on the posteroventral margin a row of backward and slightly outward pointing teeth; pereopod 2 article 2 carries medially along the anterior margin a number of short, pointed, proximally inflated, hollow setae, (Just, 1984a, figs 13–14, 16; this paper Fig. 8). When pereopod 2 is moved forward the setae come into contact with the coxal plate teeth. This may result in the production of sound. The different arrangement of setae in the three species (*A. crassicornis*: nearly straight row, *A. magellani*: on two projecting lobes, *A. trilobatus*: on three projecting lobes) further suggests differences in the sound patterns produced. Stridulation in live animals has not been observed.

In this paper the three species are placed in *Ambicholestes* s.s. together with *A. squamiferus, A. cygnatratus* n.sp. and *A. poorei* n.sp. for other reasons, but their joint possession of a unique potential stridulation mechanism suggests they form a clade which may eventually warrant separate genus group recognition.

Sexual dimorphism

Some groups of siphonoecetines exhibit distinctive sexual dimorphism (*Siphonoecetes (Centraloecetes)*: uropod 1, Just, 1983; *Australoecetes (Stebbingoecetes)*: coxal plate 1, Just, 1985; *Africoecetes*: pereopod 2, Just, 1984b). No such differences between the sexes have been observed in species of *Caribboecetes* or *Ambicholestes*. In species of *Ambicholestes*, as in all other siphonoecetines, male antennae are longer, antenna 1 often with more flagellar articles, stouter, and more densely setose than in females; the body length of adult males is greater than in adult females; and females often have fewer robust setae on pereopods and uropods. The number of robust setae mentioned in descriptions below is the maximum number found in adult males, or otherwise in the material available.

Ambicholestes n.gen.

Diagnosis. Concholestid Siphonoecetinae (*sensu* Just, 1988) with inner ramus of uropod 1 at most ½ length of outer ramus, flattened, with robust setae on margin. Uropod 3 without ramus. Mandibular palp blunt or pointed, with or without small second article. Inner lobes of lower lip complexly lobate. Ocular field of eye lobes inflated. Article 2 of pereopod 7 with marginal setae and midlateral, single, longitudinal row of setae. Oostegites on pereopods 2–5. Gills on pereopods 4–6.

Type species. *Caribboecetes magellani* Just, 1984a.

Additional species. *Ambicholestes berentsae* n.sp., *A. crassicornis* (Just, 1984a) **n.comb.**, *A. cygnatratus* n.sp., *A. minutus* n.sp., *A. poorei* n.sp., *A. squamiferus* (Just, 1984a) **n.comb.**, *A. thetis* n.sp., *A. trilobatus* n.sp.

Further description. Rostrum present or absent. Coxal plates 5 and 6 posterolobate only. Upper lip with apical notch. Antenna 1 article 3 55–85% length of article 1, article 1 85–95% length of article 2. Antenna 2 peduncular article 4 75–90% length of article 5. Antenna 1 reaching from middle of to just beyond peduncular article 5 of antenna 2. Pereopod 1 article 6 subequal in length to article 5 (± 10%), with or normally without posteroapical triangular tooth, with posteroapical robust seta and varying number of posterior robust setae; article 5 normally with posteroapical robust seta. Pereopod 2 article 6 subequal in length to article 5 (± 10%), with posteroapical triangular tooth and varying number of posterior robust setae; article 5 with 1 posteroapical robust seta. Pereopods 3 and 4 with

posterior short, robust setae on article 5. Pereopods 5 and 6 with crescent of short, equal-sized robust setae on article 5. Pleopods with peduncle broader than long, rami at most as long as width of peduncle, inner ramus slightly longer than outer ramus.

Distribution. The Philippines (*A. magellani, A. squamiferus*), Guam (*A. squamiferus*, new record), Caribbean (*A. crassicornis*), Australia (see Fig. 1); 0.1–229 m.

Etymology. The genus name is derived from the Latin *ambifarius* = with two sides, referring to the bimodal distribution of the genus (South East Asia-Australia and the Caribbean), combined with an allusion to its concholestid affinity. Masculinum.

Ambicholestes (Ambicholestes) squamiferus (Just, 1984a), n.comb.

Caribboecetes squamiferus Just, 1984a: 59, figs 1D, 18, 19.

Material examined. Agana Bay, Guam, on rubble, 12.8 m, 25 April 1984, Stn GUM 112D, J.H. Dominguez and R.K. Kropp, NMNH (11 specimens in small prosobranch shells). Pago Bay, Guam, under/in algal mat at outer reef flat, intertidal, 1 November 1984, Stn GUM 189, R.K. Kropp, NMNH (62 specimens in similar abodes), AM P44613 (10 specimens in similar abodes), Guam Marine Laboratory, University of Guam (10 specimens in similar abodes).

This is the first record of Siphonoecetinae from Guam.

Key to Australian *Ambicholestes* n.gen.

1 Mandibular palp 2-articulate, blunt, somewhat club shaped, reaching to about apex of incisor ..... (*Ambicholestes* sensu stricto) 2

—— Mandibular palp 1-articulate, apically pointed, overreaching incisor with at least 1/3 palp length ..... (*Austrolestes*) n.subgen. 5

2 Article 2 of pereopod 2 anterior margin with 2 or 3 anterior lobes, lobe margins with medial short, hollow setae. Coxal plate 2 posteroventral margin with row of sharp teeth 3

—— Article 2 of pereopod 2 anterior margin straight, without specialised setae. Coxal plate 2 posteroventral margin smooth 4

3 Rostrum absent. Article 2 of pereopod 2 with 2 lobes. Pleon dorsally smooth ..... *(Ambicholestes) magellani* (Just, 1984a)

—— Rostrum present, pointed, arising from depressed position between antennae 1. Article 2 of pereopod 1 with 3 lobes. Pleon densely setulose ..... *(Ambicholestes) trilobatus* n.sp.

4 Rostrum present in normal position. Cephalic surface in rostral area smooth ..... *(Ambicholestes) cygnatratus* n.sp.

—— Rostrum absent. Midanterior cephalic margin forming a broadly rounded setulose lobe ..... *(Ambicholestes) poorei* n.sp.

5 Triangular rostrum present in normal position 6

—— Rostrum absent. Midanterior cephalic margin forming a wide, rounded triangle ..... *(Austrolestes) thetis* n.sp.

6 Cephalon twice as long as pereonite 1. Peduncular article 3 of antenna 2 with medioproximal hook shaped robust seta ..... *(Austrolestes) minutus* n.sp.

—— Cephalon and pereonite 1 of subequal length. Antenna 2 without hook shaped robust setae ..... *(Austrolestes) berentsae* n.sp.

Subgenus *Ambicholestes* s.s.

Diagnosis. *Ambicholestes* with short, club-shaped mandibular palp carrying tiny second article; palp reaching to about apex of incisor. Antenna 1 article 3 55–70% length of article 1. Male antenna 2 at most as long as cephalon and pereon combined.

Type species. *Caribboecetes magellani* Just, 1984a.

Additional species. *Ambicholestes crassicornis* (Just, 1984a) **n.comb.**, *A. cygnatratus* n.sp., *A. poorei* n.sp., *A. squamiferus* (Just, 1984a) **n.comb.**, *A. trilobatus* n.sp.

Ambicholestes (Ambicholestes) cygnatratus n.sp.

Figs 3–5

Material examined. HOLOTYPE: male, 2.5 mm, Bush Bay, 5 km off shore, 30 km S of Carnarvon, 29°10'S 114°39'E, 2 m, extensive shallow sea-grass beds and detritus, airlift, 6 January 1984, R.T. Springthorpe & J.K. Lowry, Stn WA-431, AM P44599. PARATYPES: (77 specimens, all from Western Australia). Same data as holotype, AM P34966 (28 specimens). One kilometre W of Red Bluff, Kalbarri, 27°42'S 114°09'E, 18 m, *Ecklonia* bed, rocky bottom, "curly" bryozoans, 9 January 1984, J.K. Lowry, Stn WA-452, AM P34967 (4). Green Island, Rottnest Island, 32°01'S 115°S 30'E, off jetty, 0.5 m, coralline algae at base of jetty pilings, 21 December 1983, R.T. Springthorpe, AM P34968 (1). Kalbarri, 500 m off Chinaman's Rock, 27°42'S 114°09'E, 6 m, rocky bottom, "curly pink" bryozoans, 10 January 1984, R.T. Springthorpe, Stn WA-460, AM P34979 (18). Kalbarri, 500 m off Chinaman's Rock, 27°42'S 114°09'E, 6 m, brown algae on rock shelf, 10 January 1984, J.K. Lowry, Stn WA-465, AM P34980. Kalbarri, Red Bluff, 27°42'S 114°09'E, 3–4 m, rocky shore, mixed coralline algae, 10 January 1984, R.T. Springthorpe, Stn WA-480, AM P34981. Cathedral Rock, Rottnest Island, 32°01'S 115°27'E, 1 m, edge of reef flat, mixed algae and sponges, 21 December 1983, R.T. Springthorpe and J.K. Lowry, Stn WA-250, AM P34982 (1). Green Island, Rottnest Island, 32°01'S 115°30'E, off jetty, 1 m, mixed algal turf on rock, 21 December 1983, R.T. Springthorpe, Stn WA-268, AM P35070 (2). Cape Range National Park, off Ned's Camp, channel in Ningaloo Reef, 21°59'S 113°54.5'E, 6 m, tubular brown algae, 31 December 1983, R.T. Springthorpe, Stn WA-320, AM P35074 (2). Cape Range National Park, off South Ned's Beach, 22°00'S 113°55'E, inshore limestone reef, 2 m, mixed algae, 31 December 1983, J.K. Lowry, AM P35076 (2). North side of Point John, Rockingham, 30 km S of Perth, 0.75 m (LW), sand with some detritus, inside sea-grass and algal belt, hand dredge, 8 March 1984, J. Just, Stn AU-7, ZMUC (1). Denham, Shark Bay, near head of jetty (east side), along edge of dense *Posidonia* bed, 2 m (MW), sand, foraminiferans, detritus, hand dredge, 21 March 1984, J. Just, Stn AU-19, ZMUC (3).

Diagnosis. Rostrum present in normal position. Antennal peduncles with smooth cuticle (not counting ordinary setae).

Further description. Rostrum short, triangular. Subrostral part of frons with microsetules. Antennal peduncles without robust setae. Antenna 2 ventroapical projection of article 2 as long as broad, rounded, with 3–5 apical setae.

Coxal plates 5 and 6 posterior lobe rounded with upward turned part rounded. Posterior lobe of coxal plate 7 microsetulose. Pleonal sideplates 1 and 2 evenly rounded.

Mouthparts normal. Mandibular palp laterally and distally with very dense cover of microsetules hiding tiny second article.

Pereopod 1 article 6 without posterodistal tooth, with up to 4 posterior robust setae. Pereopod 2 article 6 with up to 4 posterior robust setae, article 2 with straight anterior margin carrying a few long and a few short setae.

Uropod 1 outer ramus 3 times longer than broad, with up to 5 lateral robust setae; inner ramus half the length of outer ramus, with apical and lateral robust setae.

Urosomites 1 and 2 separate or partly fused dorsally (fusion appears to be more common in larger specimens). Telson free.

Size. Largest male: 3.1 mm; largest female: 2.8 mm.

Colour (specimens from Denham, Stn AU-19). Cephalon semitransparent with light brown shining through, with light beige bar between eyes and onto rostrum. Dorsum light brown in mottled, reticulate pattern. Eyes white with black ommatidia. Antennae colourless transparent with white blotches and dots. Coxal plates, pereopods and urosome colourless transparent.

Biology. Specimens were found on detritus-enriched sand in and around sea-grass and algal beds, in low algal mats, and under large algae on hard substrate. The only type of abode observed (most specimens listed above) is small prosobranch shells with a short coarse-grained entrance tube.

Distribution. Western Australia; 0.5–18 m depth.

Etymology. The specific epithet refers to the black swan, *Cygnus atratus*, the state symbol of Western Australia.

Ambicholestes (Ambicholestes) magellani (Just, 1984a), n.comb.

Caribboecetes magellani Just, 1984a: 57, figs 1C, 16, 17.

Material examined (237 specimens). Heron Island, south Queensland, reef crest, boulder zone, 30 September 1979, N.L. Bruce, QM W11667 (1 specimen). Heron Island, south Queensland, centre of Wistari-Heron channel, 33 m, 2 October 1980, Boer & Hensby, AM P30981 (1). Lizard Island, north Queensland, BK-119, AM P34958 (4). Lizard Island, north Queensland, BK-122, AM P34959 (4). Lizard Island, north Queensland, BK-130, AM P34960 (5). Lizard Island, north Queensland, BK-131, AM P34961 (1). Lizard Island, north Queensland, reef edge 200 m NW of Palfrey Island, 14°40'S 145°28'E, 3 m, coral sand and rubble between bommies, 16 October 1978, J.K. Lowry, AM P34962 (1). Lizard Island, north Queensland, reef edge 200 m NW of Palfrey Island, 14°40'S 145°28'E, 3 m, sand beneath coral boulders, 16 October 1978, P.C. Ferrill, AM P34963 (19). No.5 Sandbank Reef, north Queensland, 13°45'S 144°16'E, 8–10 m, rubble washing from SW end of Reef, December 1982, I. Loch, AM P34964 (88).

Fig. 3. *Ambicholestes (Ambicholestes) cygnatratus* n.sp., holotype. Scale bar: 0.5 mm.

Escape Reef, south end, north Queensland, 15°53'S 145°49'E, 18 m, rubble washing, outer slope of shelf, 20 December 1981, I. Loch, AM P34965 (85). Elizabeth Reef, SW end, Tasman Sea, 29°57.2'S 159°01.2'E, outer reef slope near "Yoshi Maru Ikawa" wreck, 12 m, algal turf on rocky substrate, airlift, 10 December 1987, R.T. Springthorpe & J.K. Lowry, Site 30, AM P37917 (2). Lizard Island, north Queensland, 14°40'S 145°28'E, outermost reef outside Research Point, seaward face, patches of coarse sand and rubble between bommies, 8 m, hand dredge, 16 July 1984, J. Just Stn AU-37, ZMUC (7). Lizard Island, north

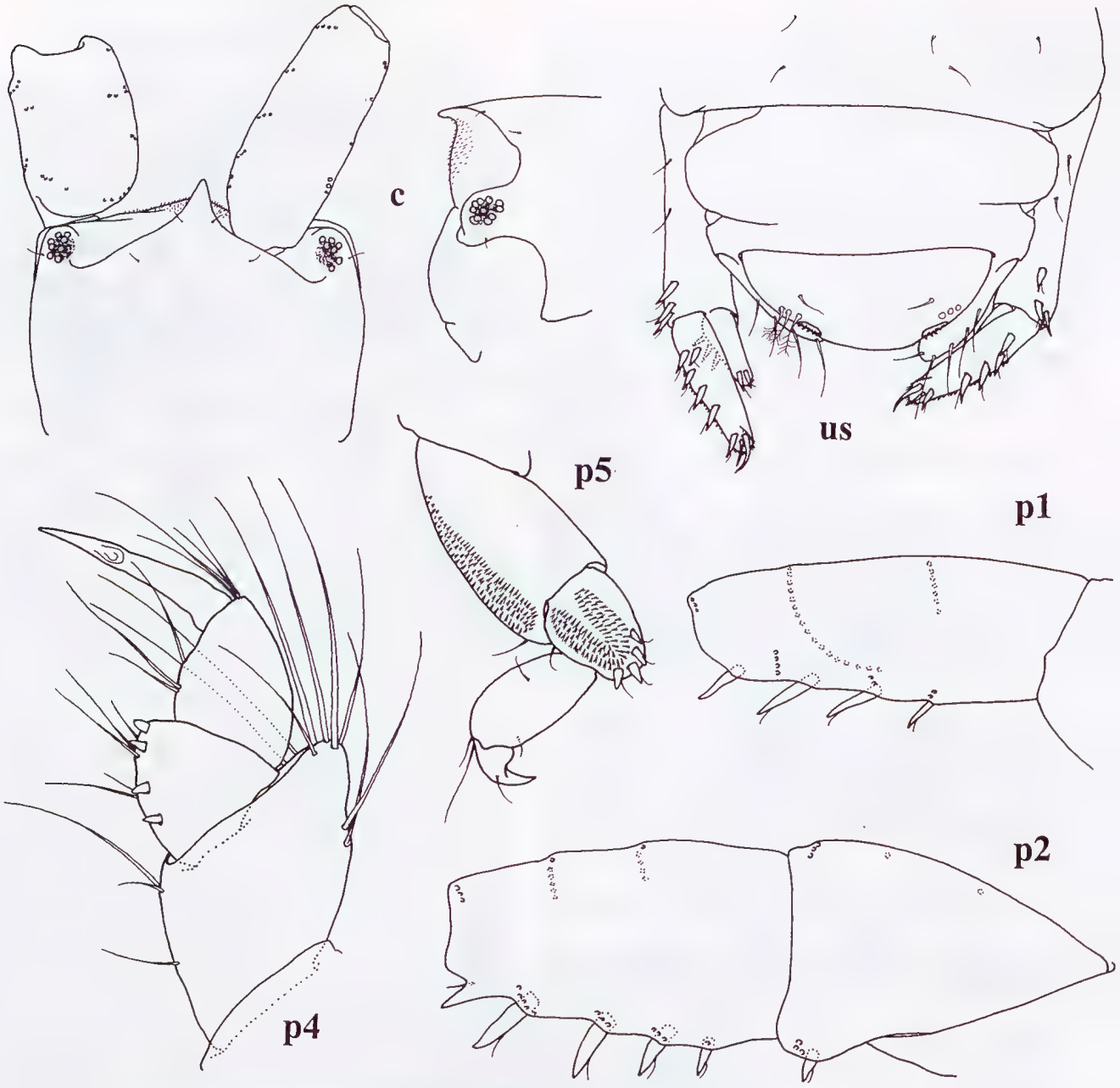

Fig. 4. *Ambicholestes (Ambicholestes) cygnatratus* n.sp., holotype. **c**, cephalon, dorsal and lateral view; **p**, pereopod (1, 2, 4 and 5); **us**, urosome, dorsal view.

Queensland, 14°40'S 145°28'E, outermost reef outside Research Point, seaward face, patches of coarse sand and rubble between bommies, 7–8 m, 17 July 1984, J. Just Stn AU-38, ZMUC (13), AM P44600 (8, in houses).

Diagnosis. Rostrum absent. Anterior margin of cephalon evenly rounded. Antenna 2 peduncle article 3 with dorsal and medial microsetules. Article 2 of pereopod 2 with anterior margin bilobed; presumed stridulation organ present.

Further description. See Just (1984a).

Remarks. The original material of *A. magellani* from The Philippines consisted of two females. Mouthparts were not dissected out for study. The present material shows that the species has complexly lobate inner lobes of the lower lip. Male cephalon and antennae are moderately longer and more setose than in females.

Australian specimens generally carry more robust setae on pereopods 3–6 article 5 than the material from the Philippines, and uropod 3 carries up to 9 lateral robust setae (2 and 3 in the holotype). These differences may represent geographical variations. In all other respects, including colour, the present material agrees with the description and illustrations in Just (1984a).

Size. Largest male: 3.3 mm (north Queensland); largest female: 2.8 (north Queensland), 3.9 mm (Heron Island).

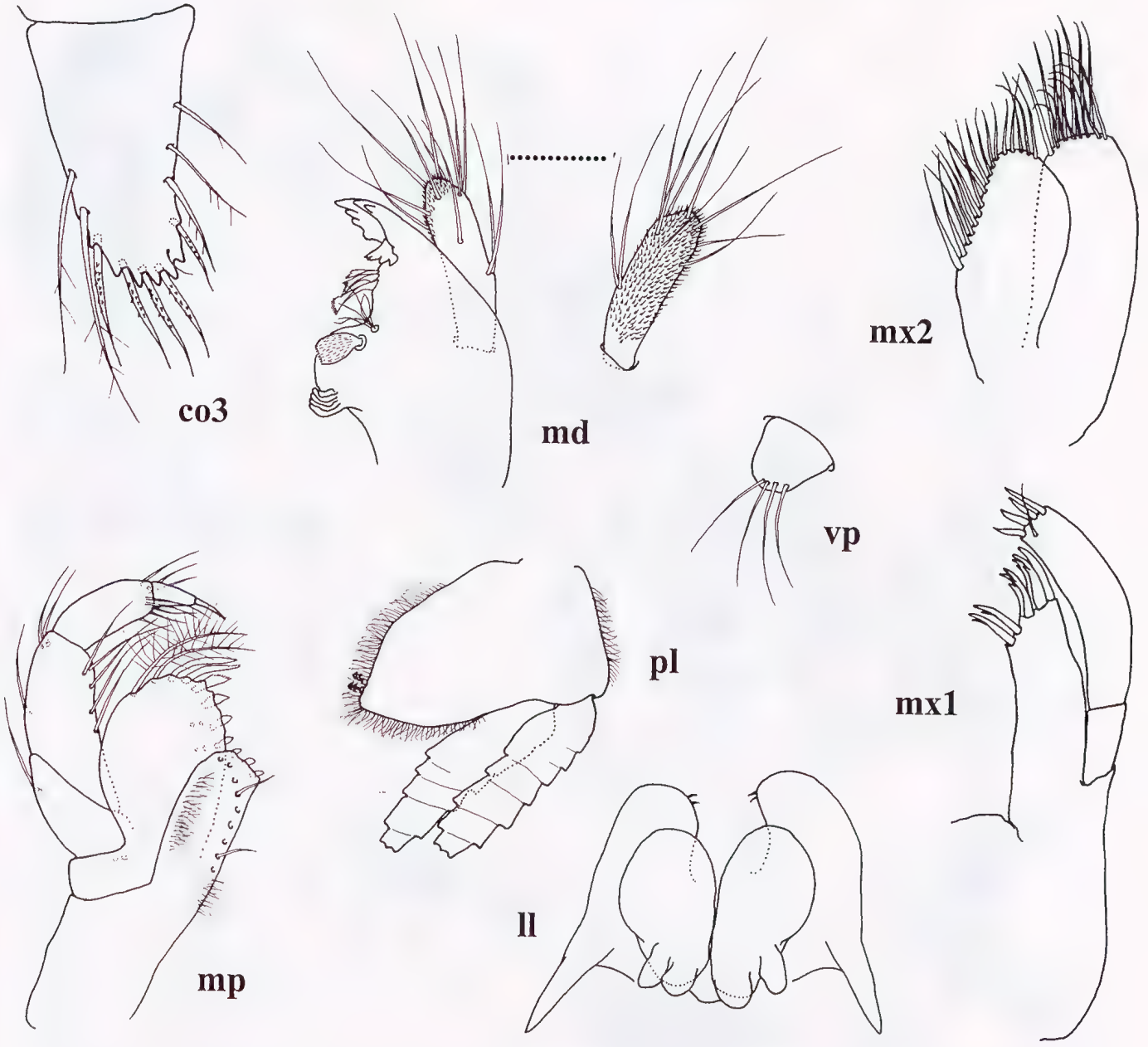

Fig. 5. *Ambicholestes (Ambicholestes) cygnatratus* n.sp., holotype. **co3**, coxal plate 3; **ll**, lower lip; **md**, mandible; **mp**, maxilliped; **mx1-2**, maxilla 1 and 2; **pl**, pleopod (ramal setae omitted); **vp**, ventral process of article 2, antenna 2.

Biology. Of the 31 specimens from Stn AU-37, AU-38 (both Lizard Island), W11667 (Heron Island) and P37917 (Elizabeth Reef) 30 were found in small prosobranch shells, each with a short, coarse-grained entrance tube. One specimen occupied a piece of calcareous polychaete tube. All other specimens listed are without their abode.

Specimens were found in sheltered places in and around coral reefs and bommies on sediments with a high content of medium to coarse coral rubble.

Distribution. Central Philippines; north-eastern Australia; 3–33 m depth.

Ambicholestes (Ambicholestes) trilobatus n.sp.

Figs 6–8

Material examined. HOLOTYPE: fully developed female, 3.5 mm, with empty marsupium, Long Island, Chesterfield Reef, Coral Sea, seaward face, 20 m, "Lady Basten", N.L. Bruce, 4 May 1979, QM W11668. Unique.

Diagnosis. Rostrum present in depressed position between antennae 1. Antenna 1 peduncle article 1 and antenna 2 peduncle article 3 (rest of antenna missing) partly covered

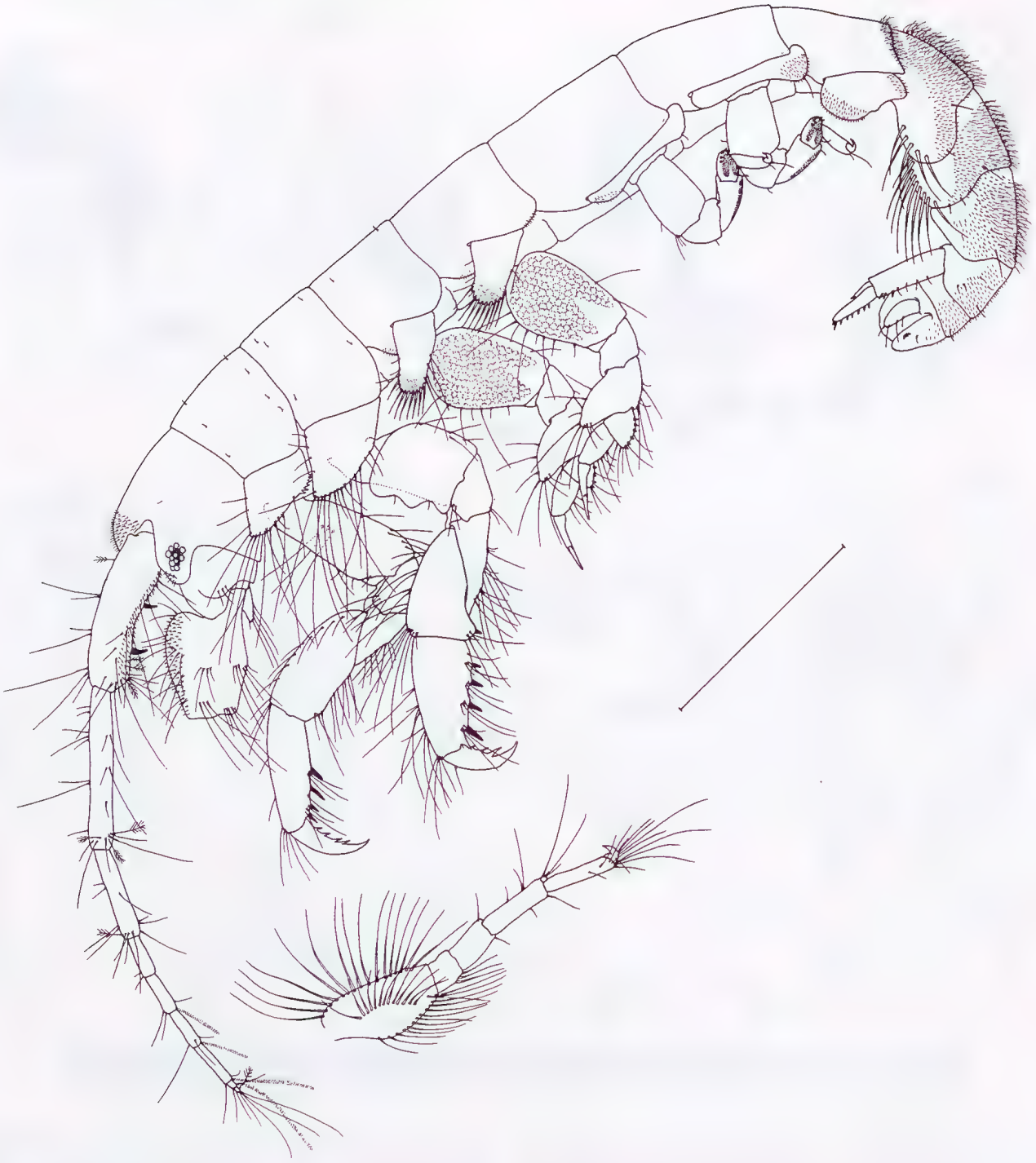

Fig. 6. *Ambicholestes (Ambicholestes) trilobatus* n.sp., holotype. Pereopod 7 shown separately. Scale bar: 0.5 mm.

with microsetules. Anterior margin of cephalon and rostrum covered by microscales. Pleon and urosomites dorsally with dense cover of long, very fine setules. Article 2 of pereopod 2 with anterior margin trilobate; presumed stridulation organ present.

Further description. Rostrum narrow, pointed. Antenna 1 peduncle article 1 with 2 recurved robust setae ventrally, with ventral to medial cover of microsetules. Antenna 2 peduncle article 3 with mid-medial robust seta, with dorsal to medial cover of microsetules; ventroapical projection of article 2 as long as wide, triangular, with 4 long lateral and 2 short medial setae.

Coxal plates 5 and 6 posterior lobe rounded with upturned part rounded. Distalmost part of plates 3 and 4, anterior lobe of plate 5, posterior lobe of plate 6, and anterior lobe of plate 7 with microscales. Pleonal sideplates 1 and 2 evenly rounded.

Mouthparts normal. Mandibular palp laterally to ventrally with lose cover of acute cuticular scales.

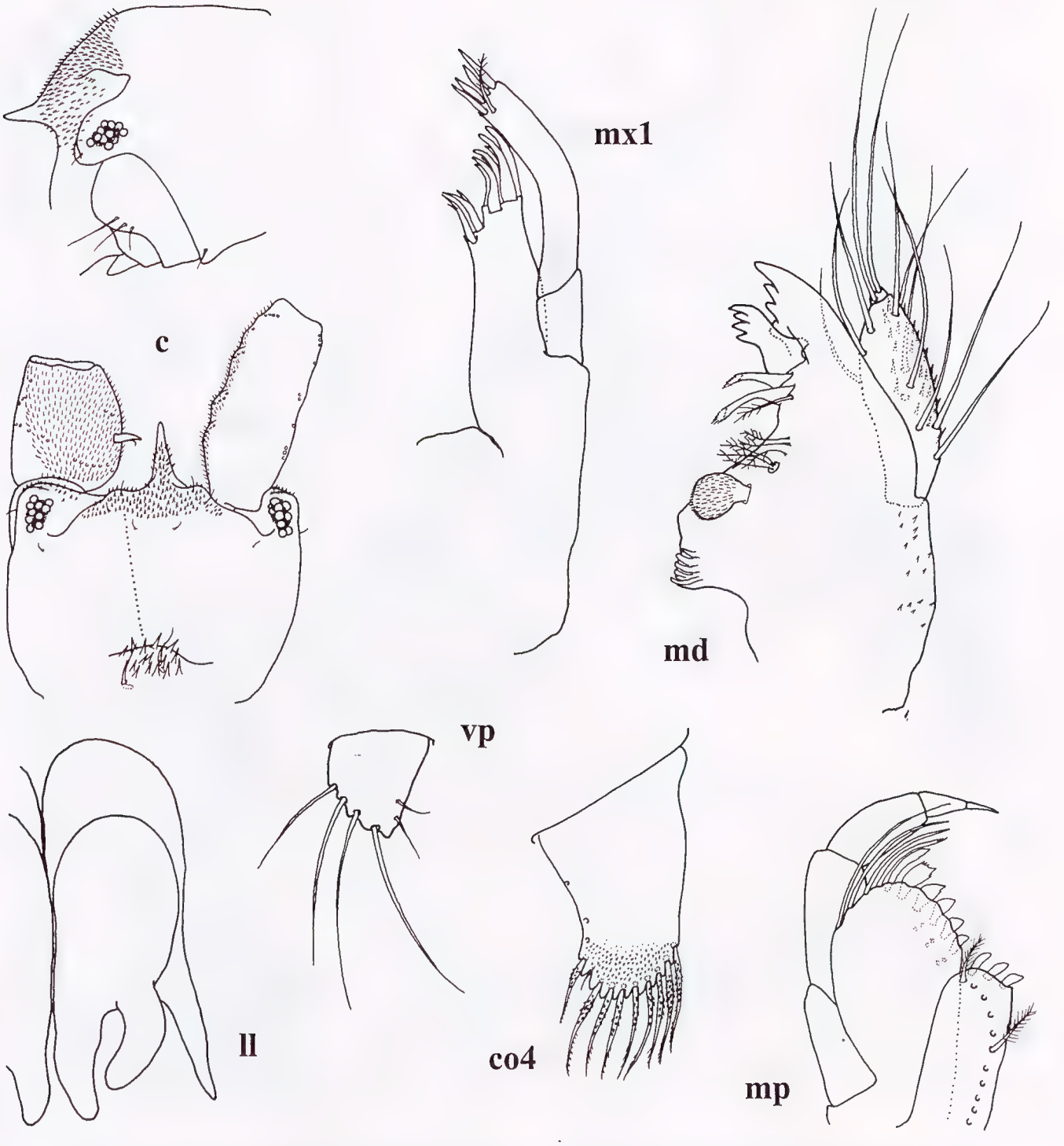

Fig. 7. *Ambicholestes (Ambicholestes) trilobatus* n.sp., holotype. **c**, cephalon, dorsal and lateral view; **co4**, coxal plate 4; **ll**, lower lip (drawn in situ); **md**, mandible; **mp**, maxilliped; **mx1**, maxilla 1; **vp**, ventral process of article 2, antenna 2.

Pereopod 1 article 6 without posterodistal tooth, with 4 posterior robust setae. Pereopod 2 article 6 with 4 posterior robust setae; article 2 anterior margin proximal to lobate part with a few small marginal teeth.

Uropod 1 outer ramus about 5 times longer than broad, with 7 lateral robust setae; inner ramus ca. 40% length of outer ramus, with lateral and apical robust setae.

Urosomites 1 and 2 free. Urosomite 3 and telson fused dorsally, but with distinct subcuticular line of articulation.

Colour and biology. Not known.

Etymology. The specific epithet alludes to the shape of the anterior margin of pereopod 2 article 2.

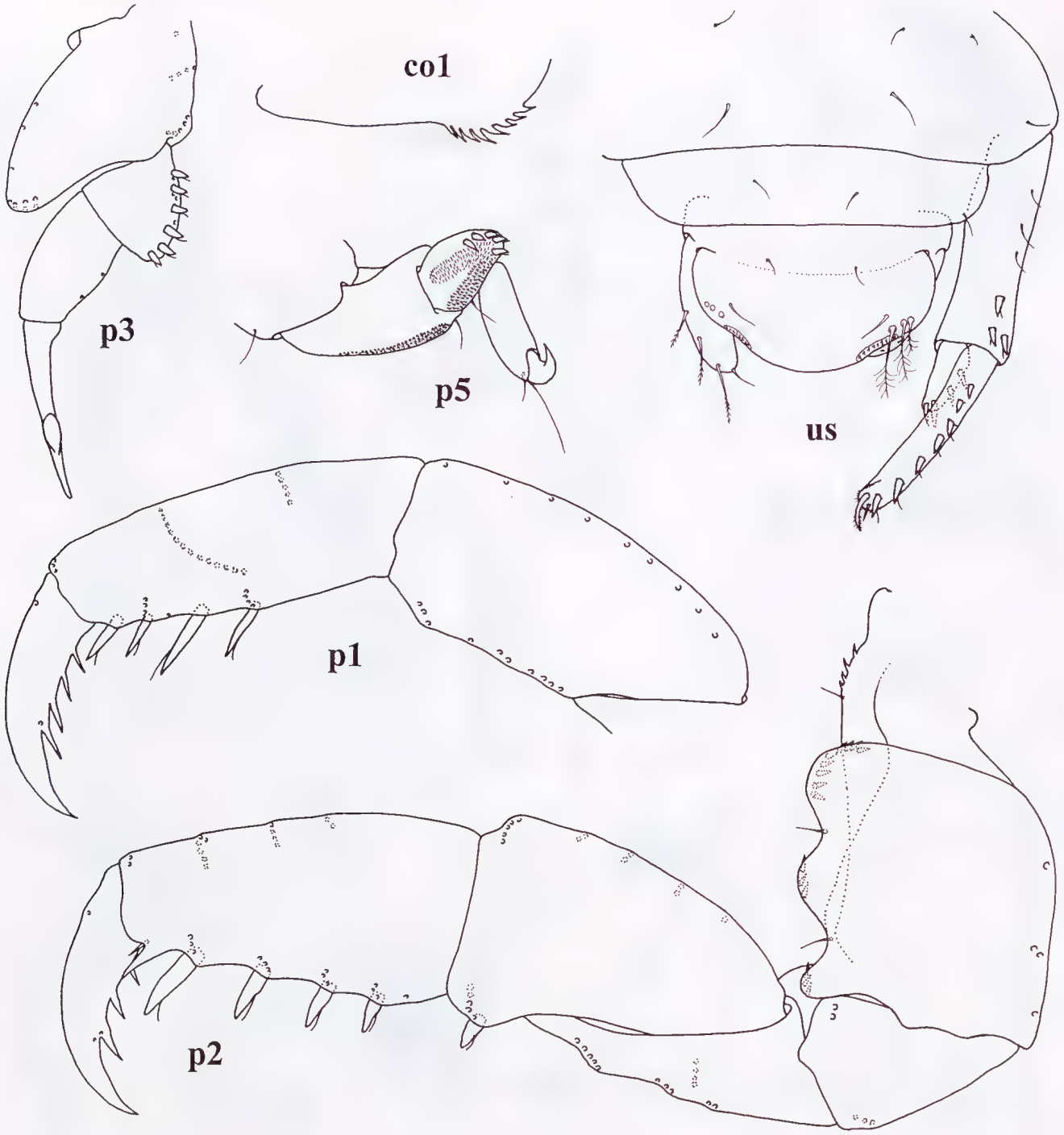

Fig. 8. *Ambicholestes (Ambicholestes) trilobatus* n.sp., holotype. **co1**, ventral margin of coxal plate 1 with posterior, presumed stridulation teeth; **p**, pereopod (1, 2, 3 and 5); **us**, urosome, dorsal view.

Ambicholestes (Ambicholestes) poorei n.sp.

Figs 9–11

Material examined. HOLOTYPE: male, 2.4 mm, Bass Strait, 40°06'S 143°16'E, 187 m, fine sand with some mud and silt, grab, G.C.B. Poore, 11 October 1980, Stn BSS 101, NMV J9544. PARATYPE: Bass Strait, 40°07'S 143°12'E, 229 m, muddy sand, grab, G.C.B. Poore, 11 October 1980, Stn BSS 105, NMV J9545 (1 male).

Diagnosis. Rostrum absent. Midanterior margin of cephalon forming a broadly rounded lobe. Antenna 1 peduncle article 1 and antenna 2 distal to peduncle article 2 with cover of microsetules. Midcephalic lobe and pleon with cover of microsetules.

Fig. 9. *Ambicholestes (Ambicholestes) poorei* n.sp., holotype. Scale bar: 0.5 mm.

Further description. Antenna 1 peduncular article 1 without robust setae, with ventral cover of microsetules. Antenna 2 peduncular article 3 with 1 midmedial robust seta, with dorsal to medial cover of microsetules; ventroapical projection of article 2 about as long as wide, rounded triangular, with a few long apical setae.

Coxal plate 4 barely longer than wide at base, plate 3 ca. 50% longer than wide. Coxal plates 5 and 6 posterior lobe with ventral part triangular, apex blunt, dorsal part rounded, not upward turned; this configuration being more pronounced in plate 6. Pleonal side plates 1 and 2 with weak posterior angle and 2 small insinuations each with a

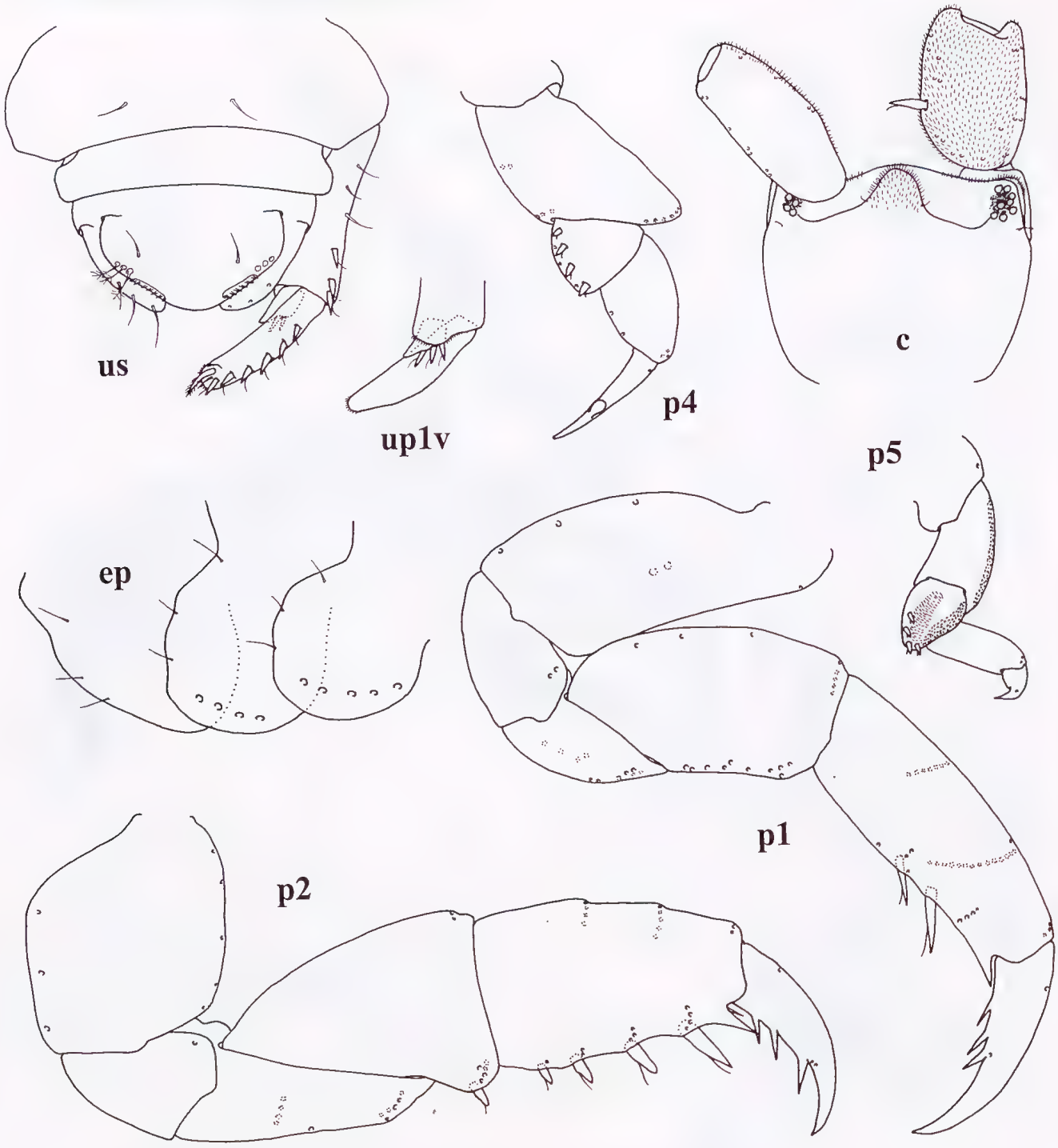

Fig. 10. *Ambicholestes (Ambicholestes) poorei* n.sp., holotype. **c**, cephalon, dorsal view; **ep**, epimeral plates, right lateral view; **p**, pereopod (1, 2, 4 and 5); **up1v**, left uropod 1 in ventral view showing inner ramus; **us**, urosome, dorsal view.

short seta below ordinary, wide sinus.

Mouthparts normal. Mandibular palp reaching to tip of incisor, with lose lateral and dorsal cover of microsetules.

Pereopod 1 article 6 with posterodistal tooth and 2 posterior robust setae; article 5 without ventrodistal robust seta. Pereopod 2 article 6 with 4 posterior robust setae; article 2 anterior margin convex, with a few long and short setae. Pereopod 7 article 2 with lateral setal row unusually short, composed of 2 setae only.

Uropod 1 outer ramus about 3 ½ times longer than broad with up to 6 lateral robust setae; inner ramus ca. ⅓ length of outer ramus, with rounded medioapical projection and

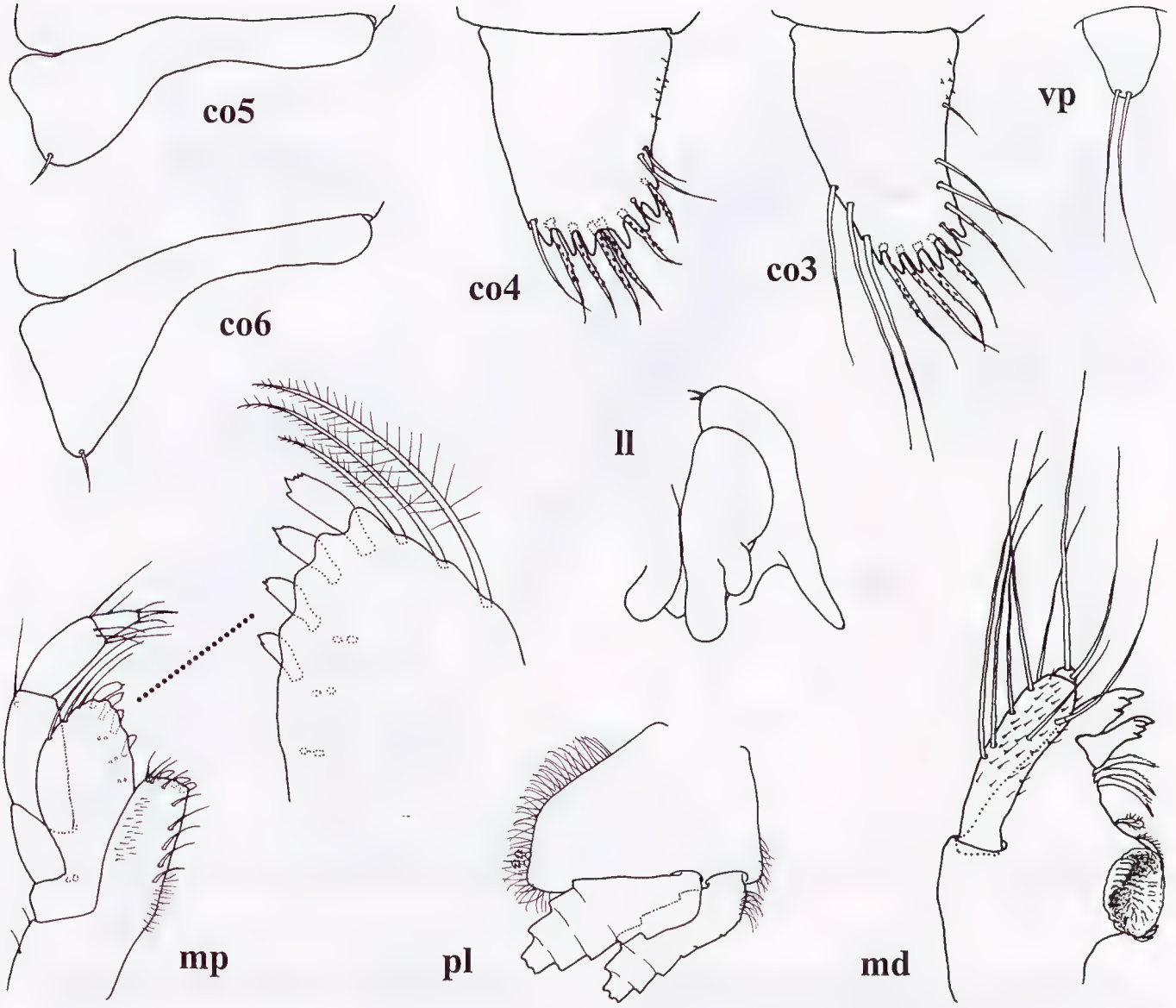

Fig. 11. *Ambicholestes (Ambicholestes) poorei* n.sp., holotype. **co**, coxal plate (3–6); **ll**, lower lip; **md**, mandible; **mx**, maxilliped; **pl**, pleopod (ramal setae omitted); **vp**, ventral process of article 2, antenna 2.

lateral robust setae only. Urosomites 1 and 2 free. Urosomite 3 and telson fused dorsally.

Size. Largest male: 2.4 mm; female not known.

Colour. Not known.

Biology. On muddy-silty sand.

Distribution. Western Bass Strait; 187–229 m depth.

Etymology. The species is named for Dr Gary Poore (Museum of Victoria) for his role in the exploration of the Bass Strait benthic fauna.

Ambicholestes (Ambicholestes) sp. A

Fig. 12

Material examined. Male, 2.3 mm, Bass Strait, 38°32'S 142°28'E, 52 m, medium sand, G.C.B. Poore, 20 November 1981, Stn BSS 187, NMV J9546.

The single specimen, which has lost both pairs of antennae, is very similar to *A. (A.) poorei* described above. It shares with that species all characteristics except the following: coxal plate 3 twice as long as wide at base; plate 4 50% longer than wide; coxal plates 5 and 6 with posterior lobe rounded ventrally, with dorsal part upward turned, rounded; pereopod 7 article 2 with row of 6 mediolateral setae.

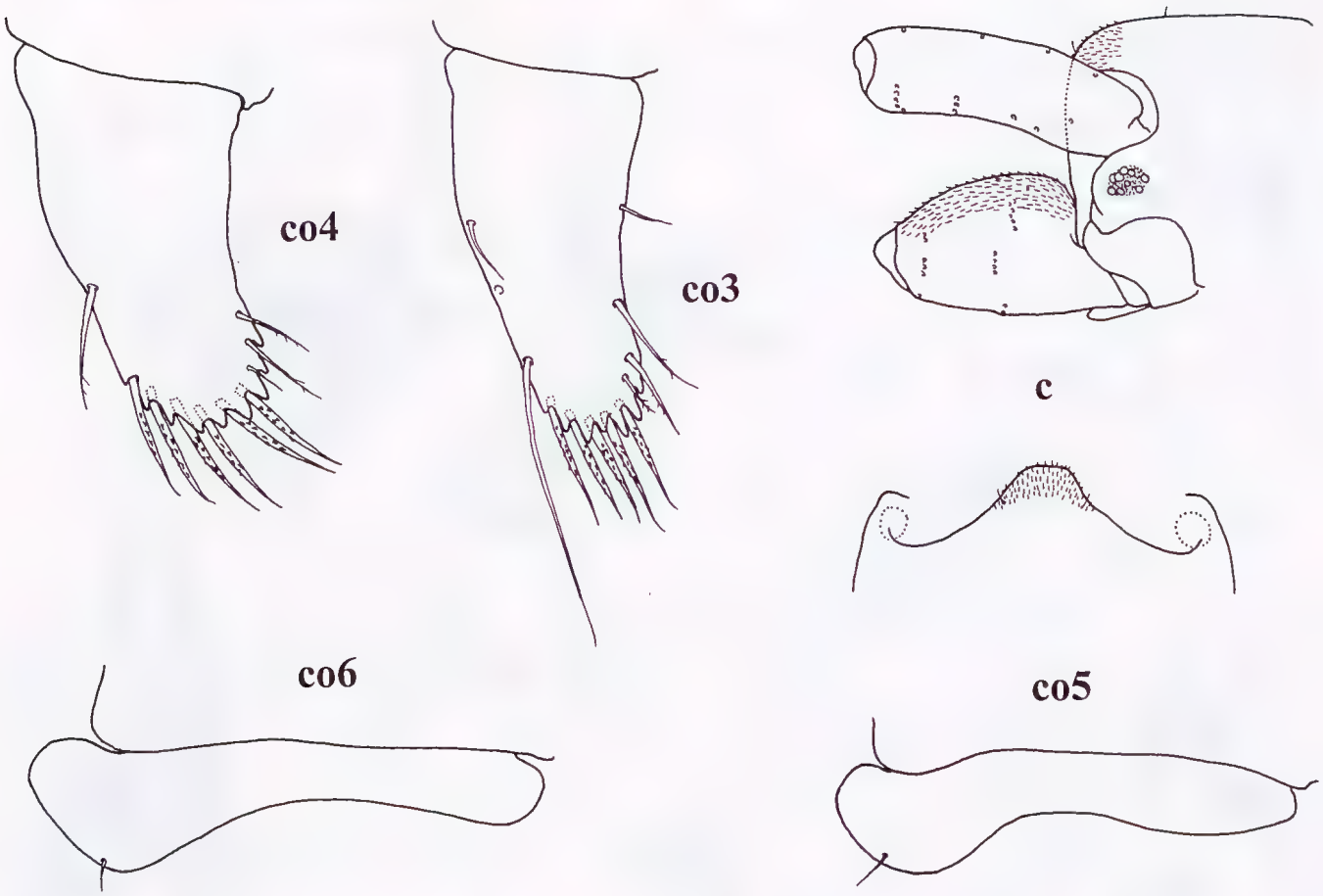

Fig. 12. *Ambicholestes (Ambicholestes)* sp. A, NMV J9546. **c**, cephalon, dorsal and lateral view; **co**, coxal plate (3–6).

Ambicholestes (A.) sp. A is probably distinct from but closely related to *A. poorei*. However, more material of both is needed before this question can be adequately addressed.

Subgenus *Austrolestes* n.subgen.

Diagnosis. *Ambicholestes* with elongate, 1-articulate, apically pointed mandibular palp; palp overreaching mandibular incisor by 1/3–1/2 palp length. Antenna 1 peduncle article 3 70–85% length of article 1. Male antenna 2 at least as long as combined length of cephalon, pereon and pleon.

Type species. *Ambicholestes berentsae* n.sp.

Additional species. *Ambicholestes minutus* n.sp., *A. thetis* n.sp.

Etymology. The name of this subgenus is composed of an allusion to Australia and its concholestid affinity.

Ambicholestes (Austrolestes) berentsae n.sp.

Figs 13–16

Concholestes spp., Stephenson & Cook (1977, partim, see Just 1988), Stephenson, Cook & Newlands (1978, partim, see Just 1988).

Material examined. HOLOTYPE: male, 5.6 mm, Jervis Bay, New South Wales, off Moona Moona Creek, 35°03'S 150°42'E, 8 m, air-lift of bottom sediment, P.B. Berents, 29 January 1983, AM P44601. PARATYPES: 265 specimens. **Jervis Bay** (136): SE of Huskisson, off Moona Moona Creek, 8 m, fine sand with detritus to coarse shelly, broadly rippled sand , just inside low rock reef covered with large brown algae, hand dredge (SCUBA), J. Just, 15 November 1984, Stn AU-65, AM P44602 (3) and ZMUC (5). North side of Plantation Point, 35°04'S 150°32'E, 5 m, wide patches of silty sand with *Halodule* between rock reefs, hand dredge (SCUBA), J. Just, 17 November 1984, Stn AU-70, AM P44603 (3). North side of Plantation Point, 35°04'S 150°32'E, 5 m, wide patches of silty sand with *Halodule* between rock reefs, hand dredge (SCUBA), J. Just, 17 November 1984, Stn AU-71, AM P44604 (3). Off Moona Moona Creek, 53°03'S 150°42'E, 8 m, sand, airlift, P.B. Berents, 17 November 1981, AM P44605

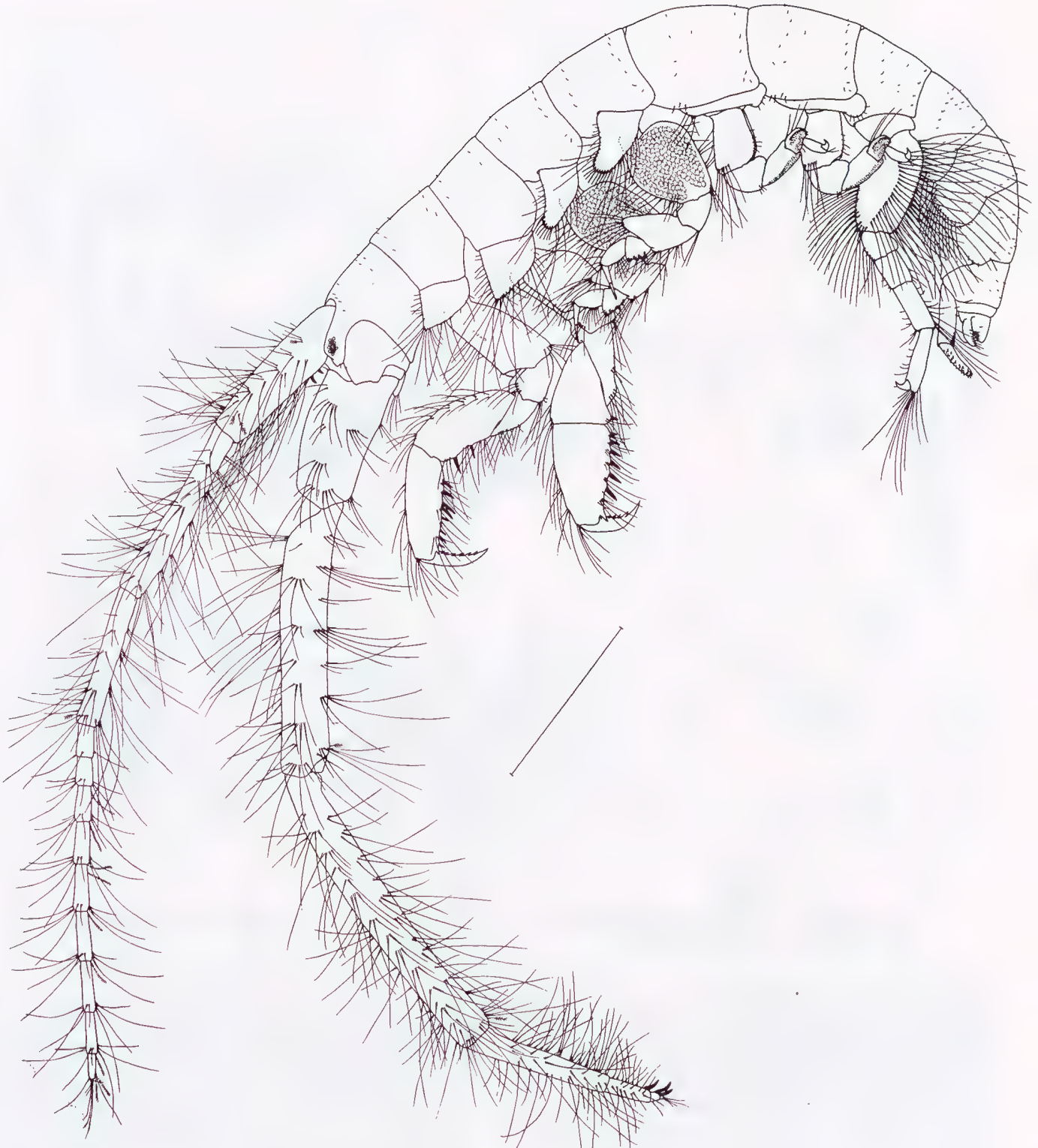

Fig. 13. *Ambicholestes (Austrolestes) berentsae* n.sp., holotype. Scale bar: 1 mm.

(3). Off Moona Moona Creek, 53°03'S 150°42'E, 8 m, sand, airlift, P.B. Berents, 17 December 1982, AM P44606 (74). Off Moona Moona Creek, 53°03'S 150°42'E, 8 m, sand, airlift, P.B. Berents and A.R. Jones, 18 March 1983, AM P44607 (16). Off Moona Moona Creek, 53°03'S 150°42'E, 8 m, sand, airlift, P.B. Berents, 29 January 1983, AM P44608 (29). Off Moona Moona Creek, 53°03'S 150°41'E, 8 m, sand, hand operated corer, P.B. Berents, 16 December 1983, AM P44609 (3). **Port Jackson** (98): North Harbour, at base of jetty at Store Beach, 33°51'S 151°16'E, 3 m, sand, large amount of fine shell fragments, some detritus, *Halodule* and various low algae, hand dredge (SCUBA), J. Just, 26 September 1984, Stn AU-59, AM P44610 (57) and P44611 (9). North Harbour, at base of jetty at Store Beach, 33°51'S 151°16'E, 3 m, sand, large amount of fine shell fragments, some detritus, *Halodule* and various low algae, hand dredge (SCUBA), J. Just, August 1986, AM P44612 (32). **Bass Strait** (27): western

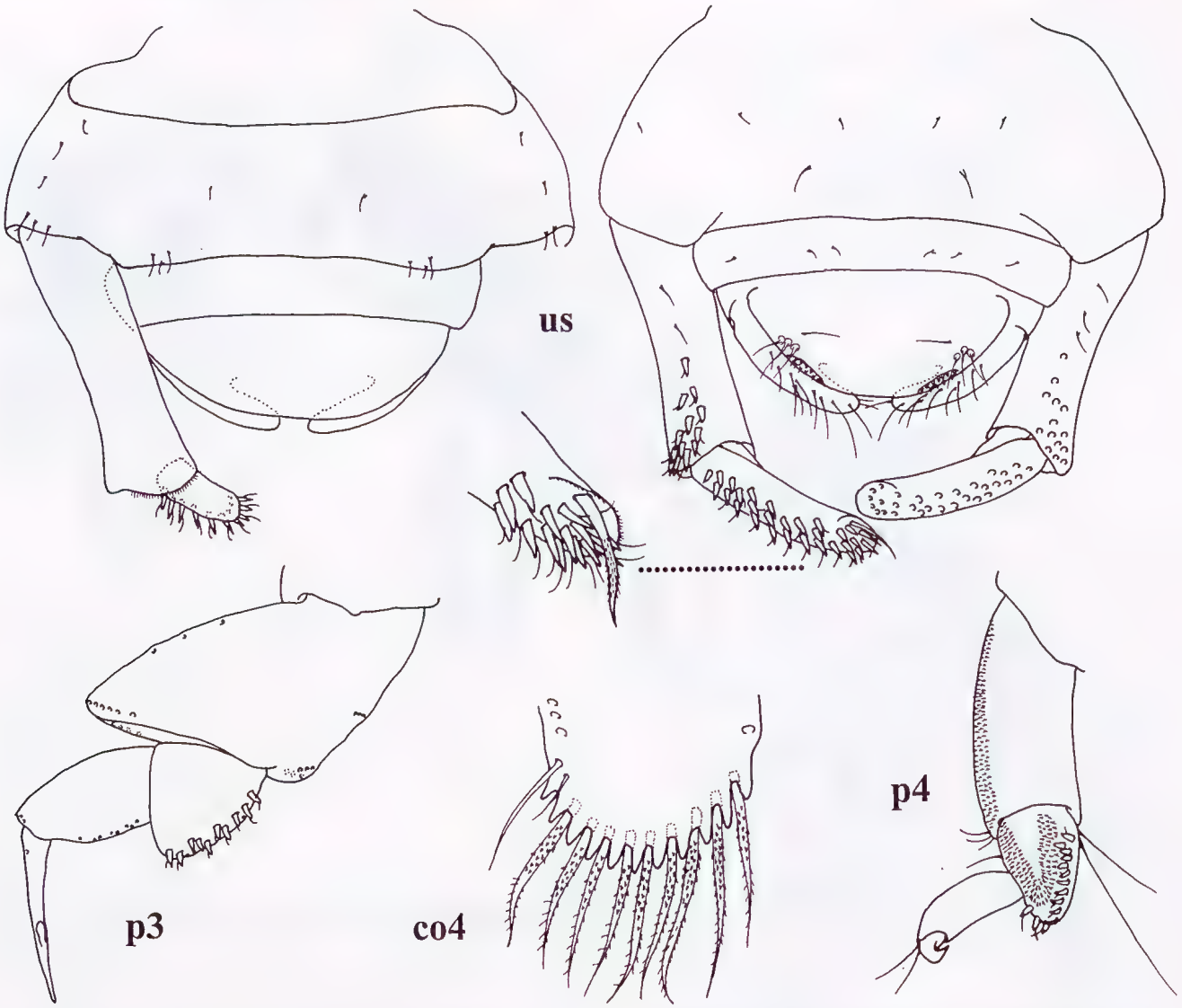

Fig. 14. *Ambicholestes (Austrolestes) berentsae* n.sp., holotype. **co4**, apex of coxal plate 4; **p**, pereopod (3 and 4); **us**, urosome, dorsal and ventral view.

Bass Strait, 64 km WNW of Cape Farewell, King Island, 39°31'S, 143°12'E, 122 m, medium sand, Smith-McIntyre grab/pipe dredge, G.C.B. Poore, HMAS "Kimbla", 11 October 1980, Stn BSS 83, NMV J9535 (1). Eastern Bass Strait, 94 km NE of North Point, Flinders Island, 38°53.7'S 147°55.2'E, 71 m, medium sand, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 15 November 1981, Stn BSS 171 S, NMV J9538 (1). Eastern Bass Strait, 70 km N of North Point, Flinders Island, 39°05.2'S 147°56.6'E, 62 m, shelly sand, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 17 November 1981, Stn BSS 172 S, NMV J9531 (1). Eastern Bass Strait, 70 km N of North Point, Flinders Island, 39°05.2'S 147°56.6'E, 62 m, shelly sand, grab, sled or trawl (see label), R. Wilson, RV "Tangaroa", 17 November 1981, Stn BSS 172, NMV J9539 (1). Western Bass Strait, 15 km S of Port Fairy, 38°32.0'S 142°28.6'E, 52 m, medium sand, grab, sled or trawl (see label), R. Wilson, RV "Tangaroa", 20 November 1981, Stn BSS 187, NMV J9543 (1). Western Bass Strait, 80 km SSE of Cape Otway, 39°26'S 142°57'E, 113 m, medium sand, Smith-McIntyre grab/pipe dredge, G.C.B. Poore, HMAS "Kimbla", 9 October 1980, Stn BSS 67, NMV J9534 (1). Western Bass Strait, 31 km SSW of Cape Otway, 39°08'S 143°24'E), 77 m, medium sand, Smith-McIntyre grab/naturalist's dredge, G.C.B. Poore, HMAS "Kimbla", 8 October 1980, Stn BSS 56, NMV J9533 (1). Central Bass Strait, 36 km S of Cape Otway, 39°03'S 143°51'E, 85 m, medium sand, carbonate, Smith-McIntyre grab/naturalist's dredge, G.C.B. Poore, HMAS "Kimbla", 7 October 1980, Stn BSS 47, NMV J9532 (1). Central Bass Strait, 38 km SW of Cape Paterson, 38°56.4'S 145°16.6'E, 70 m, fine sand, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 12 November 1981, Stn BSS 155 S, NMV J9537 (6). Central Bass Strait, 38 km SW of Cape Paterson, 38°55.5'S 145°17.0'E, 70 m, fine sand, Smith-McIntyre grab, R. Wilson, RV "Tangaroa", 12 November 1981, Stn BSS 155 G, NMV J9536 (3). Eastern Bass Strait, 20 km SE of Port Albert, 38°43.4'S 146°56.9'E, 26 m, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 18 November 1981, Stn BSS 178 S, NMV J9541 (3). Eastern Bass Strait, 20 km SE of Port Albert, 38°43.4'S 146°56.9'E, 26 m, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 18 November

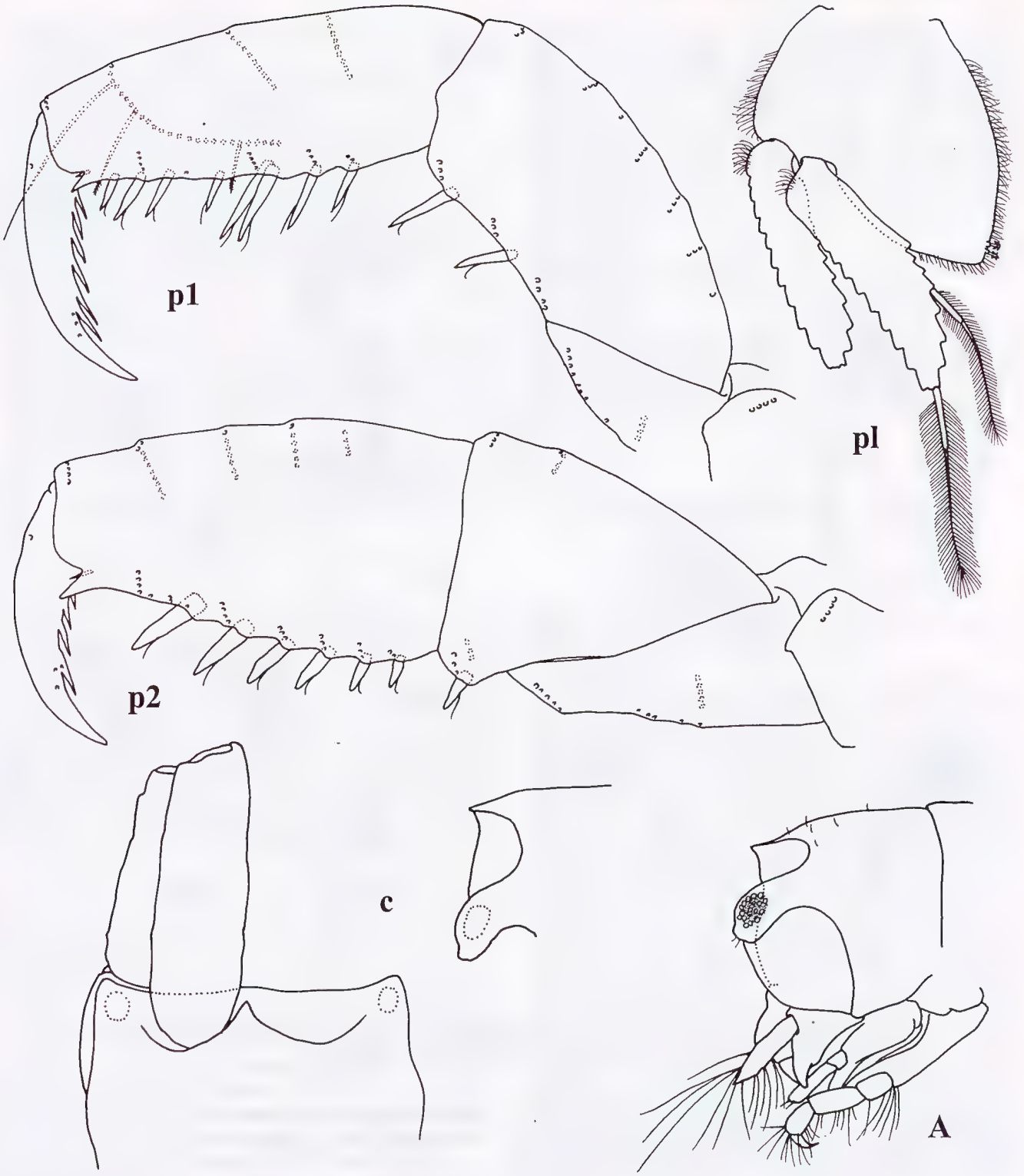

Fig. 15. *Ambicholestes (Austrolestes) berentsae* n.sp., holotype, except **A**: lateral view of cephalon of male from AU-59 (Port Jackson). **c**, cephalon, dorsal and lateral view; **p**, pereopod (1 and 2); **pl**, pleopod 1 (most ramal setae omitted).

1981, Stn BSS 178 S, NMV J9542 (1). Eastern Bass Strait, 50 km SE of Port Albert, 38°54.3'S 147°13.4'E, 58 m, coarse shell, grab, sled or trawl (see label), R. Wilson, RV "Tangaroa", 18 November 1981, Stn BSS 176, NMV J9540 (6). **Other material:** Jibbon, New South Wales, 34°05'S 151°10'E, 50 m, sand, dredge, K. Sheard, CSIRO 12 September 1943, AM P44219 (1). East of Cape Banks, New South Wales, 33°52'S 151°23'E, 88 m, 2.5 m sledge dredge, R. Springthorpe and P.H. Colman, FRV "Kapala", Stn K80-20-11, 11 December 1980, AM P44614 (3).

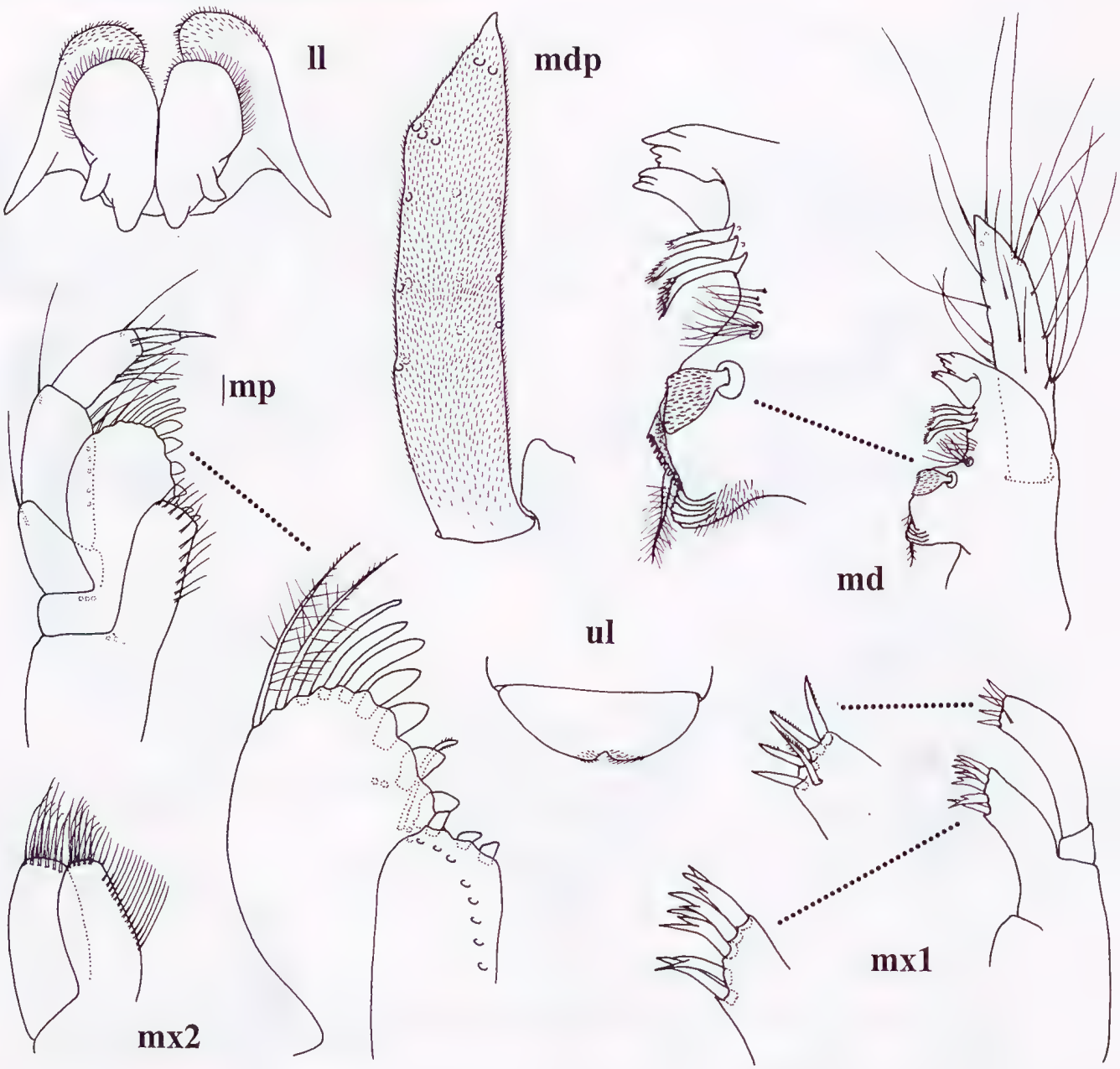

Fig. 16. *Ambicholestes (Austrolestes) berentsae* n.sp., holotype. **ll**, lower lip; **md**, mandible; **mdp**, mandibular palp, dorsolateral view; **mp**, maxilliped; **mx**, maxilla (1 and 2); **ul**, upper lip.

ADDITIONAL MATERIAL. **Moreton Bay, Queensland** (several hundred): Middle Banks, 19 m, sand, September 1972, S. Cook, Stn 9, QM W6345 (5–10 specimens, 27 abodes). Middle Banks, 22 m, sand, September 1972, S. Cook, Stn 19, QM W6346 (several hundred). Middle Banks 1982, Zool. Dep., Univ. of Queensland, Stn 1C, QM W11660 (1). Middle Banks, July/August 1982, I. Poiner, QM W11662 (10). Middle Banks, September 1976, Zool. Dep., Univ. of Queensland, QM W11663 (30). Middle Banks, October 1976, Zool. Dep., Univ. of Queensland, QM W11664 (7). Middle Banks, December 1976, Zool. Dep., Univ. of Queensland, QM W11665 (7). Middle Banks, June 1974, S. Cook and S. Newlands, QM W20646 (1).

Diagnosis. *Austrolestes* with rostrum present in normal position. Cephalon along dorsal midline as long as or up to 10% longer than pereonite 1. Cephalon and body with setules in distinct transverse rows.

Further description (type material). Rostrum pointed, triangular. Antenna 1 peduncle article 1 with 1 (occasionally 2) recurved robust setae ventrally in proximal half. Antenna 2 article 3 without robust setae; ventroapical projection of article 2 wider than long, evenly rounded, with apical row of long setae. Male antenna 1 longer than combined cephalon and pereon by approximately ½ pleon length, with up to 11 flagellar articles. Male antenna 2 about as long as cephalon, pereon and pleon combined.

Coxal plates 5 and 6 with posterior lobe rounded to bluntly triangular (plate 5 in particular); plate 5 anterior

margin with short row of long setae. Pleonal side plates 1 and 2 evenly rounded.

Mandibular palp overreaching mandibular cutting edge by about 1/2 palp length, entire lateral surface densely covered by microsetules.

Pereopod 1 article 5 with 1 (occasionally 2) posterior robust setae; article 6 with posterodistal tooth and up to 8 posterior robust setae. Pereopod 2 article 2 anterior margin straight, fringed with moderately long, simple setae; article 6 with up to 6 posterior robust setae. Pereopods 5 and 6, article 2 anterodistally with row of up to 10 long setae, article 5 with up to 15 short robust setae in crescent.

Uropod 1, peduncle with up to 15 distal robust setae; outer ramus about 4 1/2 times longer than broad, with up to 13 double and triple rows of dorsolateral robust setae; inner ramus barely less than 1/2 length of outer ramus, with up to 11 lateral and apical robust setae.

Urosomites 1 and 2 free; urosomites 2 and 3 normally free, but in some specimens part fusion is apparent; urosomite 3 and telson fused dorsally, but often with distinct subcuticular line of demarcation.

Size. Largest male: 7.7 mm; largest female: 4.8 mm.

Colour (live animals). Overall yellowish-orange. Cephalon and first two pereonites with red-brown mottling, rest of pereon and most of pleon with whitish mottling. Pereopods colourless transparent, anterior ones in large specimens with brownish tinge. Frons and mouthparts faintly brownish. Antenna 1 semitransparent whitish, with faint orange-yellow core in peduncle; peduncle and flagellum with whitish longitudinal line middorsally. Antenna 2 generally as 1, with same core colour in peduncle; peduncle articles 3–5 with 3 longitudinal lines of white and 3 of orange-brown.

Moreton Bay population. Specimens from Moreton Bay have not been included in the type material, although they identify to *A. berentsae* in the key presented. Adult specimens are significantly smaller than the type material (largest male: 4.8 mm; largest female: 3.2 mm; largest ovigerous female: 2.9 mm). Pereopods 1 and 2 are more robust, with articles 5 and 6 slightly broader relative to the length than in the type material. Generally specimens from Moreton Bay have fewer robust setae on pereopods and uropods. In some specimens the telson is separate from urosomite 3, in others partly or fully fused as in the type material.

The difference in size between specimens of the Moreton Bay population and the more southerly type material may reflect environmental differences, hydrographic regimes in particular. Morphological differences outlined may be partly size dependent and partly of a clinal nature. However, material is required from in between central New South Wales and Moreton Bay as well as around and outside Moreton Bay and north perhaps to the southern reaches of the Great Barrier Reef in order to fully assess the status of the Moreton Bay population here referred to *A. berentsae*.

Biology. On fine to coarse, often shelly, detritus-covered sand. In shallow water also in *Halodule* sea-grass beds. The predominant abode used is small prosobranch shells furnished with a short tube with coarse shell fragments (86 out of 110 abodes from Jervis Bay and Port Jackson, the several hundred abodes from Moreton Bay and the only 3 abodes found in the material from the Bass Strait). Some specimens from Jervis Bay and Port Jackson occupied small scaphopod shells (5) or polychaete tubes (19).

Distribution (all populations). Eastern Australia: Moreton Bay, Queensland, to Bass Strait; 3–122 m depth.

Etymology. This species is named for Dr P. (Penny) B. Berents, Australian Museum, in recognition of her work on the Jervis Bay fauna and her help during my field work in New South Wales, Jervis Bay in particular.

Ambicholestes (Austrolestes) thetis n.sp.

Figs 17–19

Siphonoecetes australis Stebbing, 1910 (*partim*, Stebbing 1910, Plate 54C).

Material examined. HOLOTYPE: male, 4.7 mm, Bass Strait, 63 km E of North Point, Flinders Island, 39°44.8'S 148°40.6'E, 124 m, muddy sand, epibenthic sled, R. Wilson, RV "Tangaroa", 14 November 1981, Stn BSS 167, NMV J9528. PARATYPES: 25 specimens. Eastern Bass Strait, 60 km E of North Point, Flinders Island, 39°41.7'S 148°39.5'E, 115 m, muddy sand, naturalist's dredge, G.C.B. Poore, HMAS "Kimbla", 27 March 1979, Stn BSS 32, NMV J9526 (4 specimens) and J9527 (3). Eastern Bass Strait, 63 km E of North Point, Flinders Island, Tasmania, 39°44.8'S 148°40.6'E, 124 m, muddy sand, Smith-McIntyre grab, R. Wilson, RV "Tangaroa", 14 November 1981, Stn BSS 167 G, NMV J9529 (4). Eastern Bass Strait, 63 km E of North Point, Flinders Island, Tasmania, 39°44.8'S 148°40.6'E, 124 m, fine sand, WHOI epibenthic sled, R. Wilson, RV "Tangaroa", 14 November 1981, Stn BSS 167 S, NMV J9530 (20). New South Wales, off Cape Three Point, 40–50 fms (74–92 m), "Thetis" Expedition, Stn 13, AM P2529, (1 male, one of two former syntypes of *Siphonoecetes australis* Stebbing, 1910, see Just 1985: 333). New South Wales, off Cape Three Point, 40–50 fms (74–92 m), "Thetis" Expedition, January 1911, AM P31867 (re-registered from P2528) (1 male, probably a missing syntype of *Siphonoecetes australis* Stebbing, 1910, see Just 1985: 333).

Diagnosis. *Austrolestes* without rostrum. Cephalic front margin a rounded wide triangle. Cephalon along midline as long as first 1 1/2 pereonites

Further description. Antenna 1 peduncle article 1 with 1 recurving robust seta ventrally in proximal half. Antenna 2 peduncular article 3 without robust setae; ventroapical projection of peduncular article 2 wider than long, evenly rounded, with apical row of long setae. Male antenna 1

Fig. 17. *Ambicholestes (Austrolestes) thetis* n.sp., holotype. Scale bar: 1 mm.

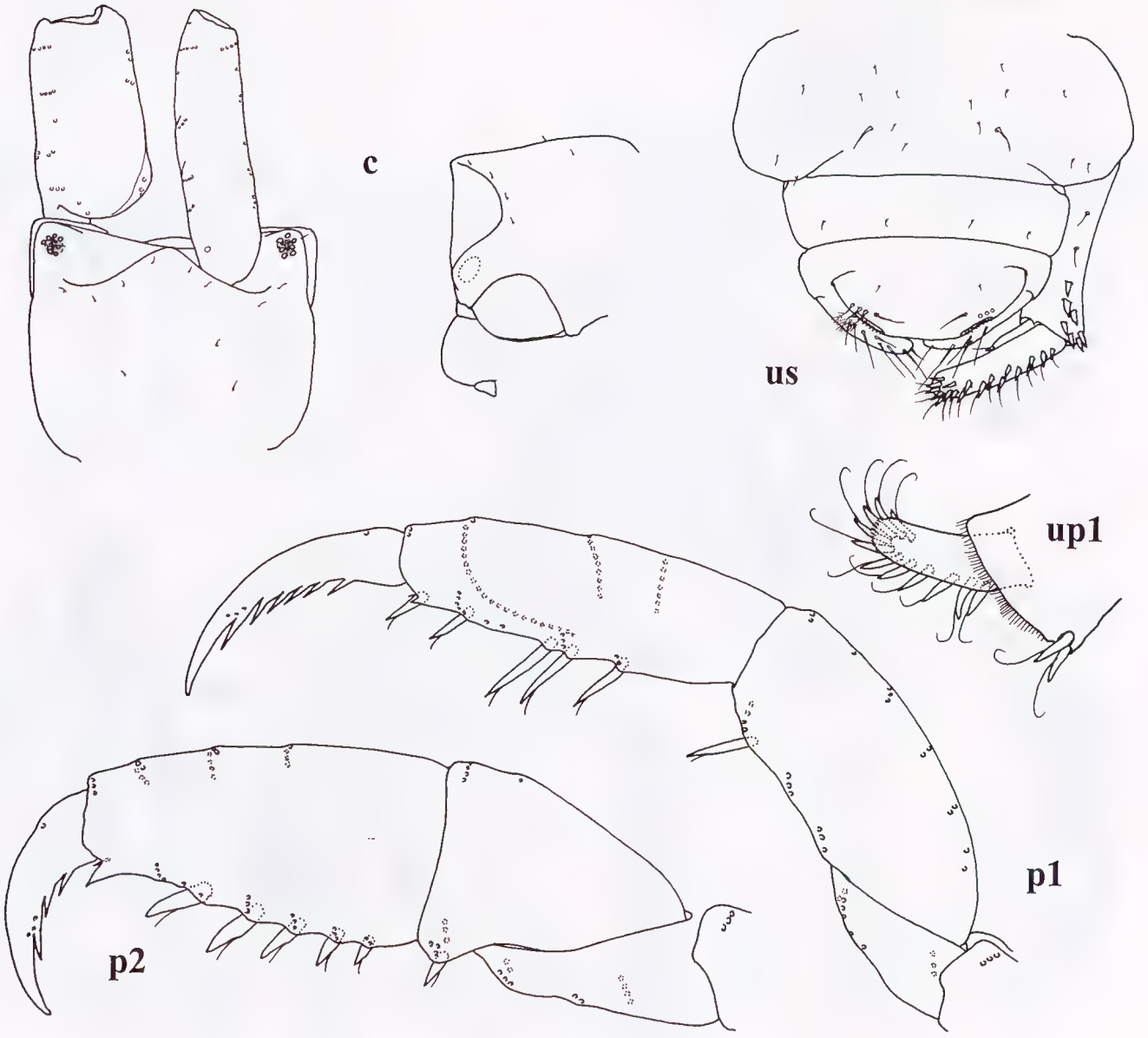

Fig. 18. *Ambicholestes (Austrolestes) thetis* n.sp., holotype. **c**, cephalon, dorsal and lateral view; **p**, pereopod (1 and 2); **up1**, left uropod 1, ventral view, inner ramus, enlarged; **us**, urosome, dorsal view.

about as long as first 6½ pereonites with up to 7 flagellar articles. Male antenna 2 as long as cephalon, pereon and pleon combined.

Coxal plates 5 and 6 with posterior lobe rounded; plate 5 without long anterior setae. Pleonal sideplates 1 and 2 evenly rounded.

Mandibular palp overreaching mandibular incisor by about 1/10 palp length, with distolateral and medioventral cover of microsetules, tip naked.

Pereopod 1 article 5 with 1 posterodistal robust seta; article 6 with small posterodistal tooth. Pereopod 2 article 2 anterior margin straight, fringed with moderately long simple setae; article 6 with up to 5 posterior robust setae. Pereopods 5 and 6 article 2 anterodistally with 1 long and a few short setae.

Uropod 1 peduncle about 2½ times longer than wide, with up to 8 distal robust setae dorsolaterally; outer ramus barely 4 times longer than broad, with 15–17 lateral robust setae, single as well as double; inner ramus c. ⅖ length of outer ramus with up to 12 lateral and apical robust setae.

Urosomites 1 and 2 free. Urosomite 3 and telson fused dorsally.

Size. Largest male: 4.7 mm; largest female: 3.8 mm.

Colour. Not known.

Biology. On muddy sand.

Distribution. Eastern Australia: central New South Wales to eastern Bass Strait; 74–124 m depth.

Etymology. The specific epithet refers to HMCS "Thetis" from which the first specimens of this species were collected off Botany Bay.

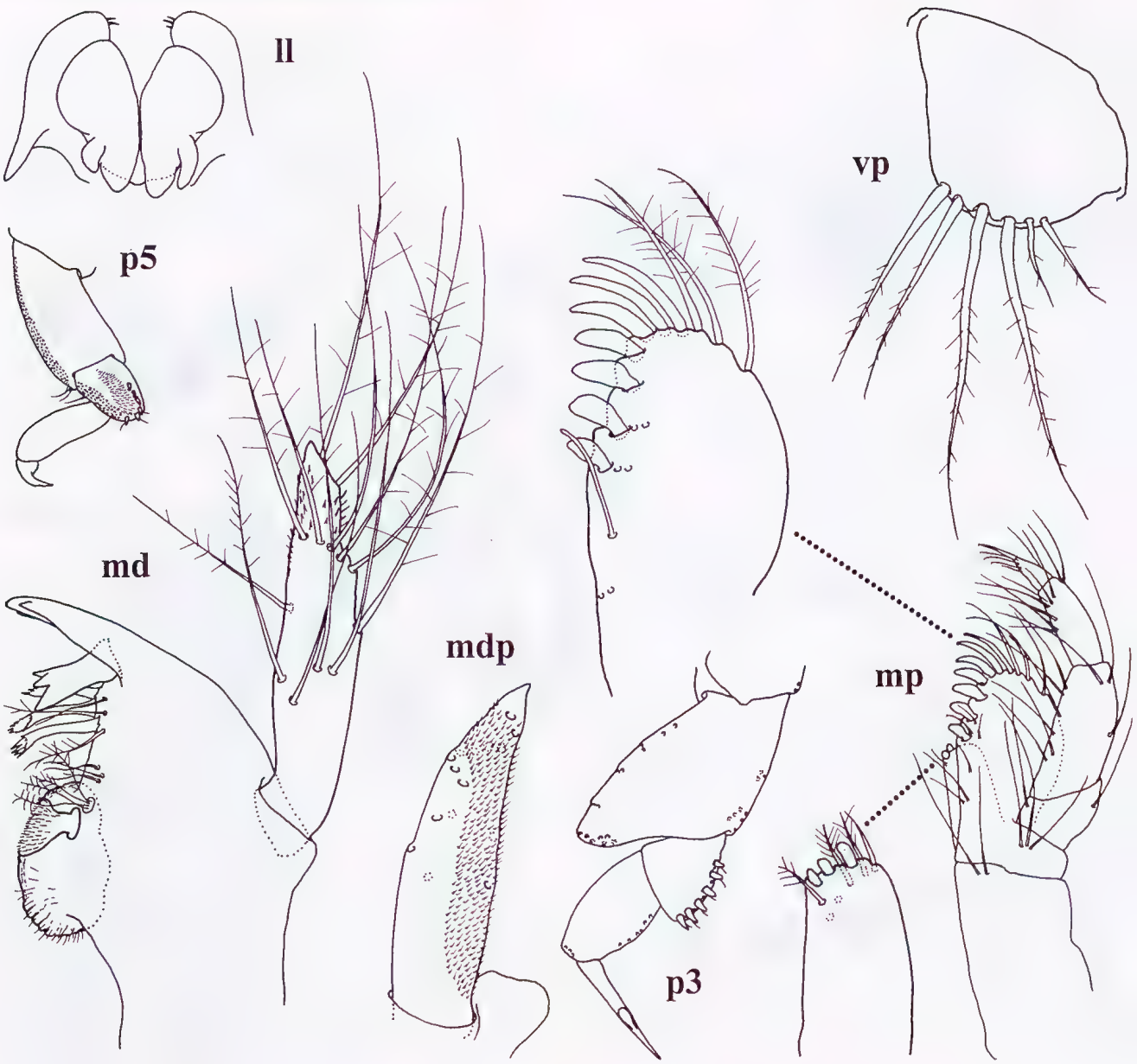

Fig. 19. *Ambicholestes (Austrolestes) thetis* n.sp., holotype. **ll**, lower lip; **md**, mandible: **mdp**, mandibular palp, dorsolateral view; **mp**, maxilliped; **p**, pereopod (3 and 5); **vp**, ventral process of article 2, antenna 2.

Ambicholestes (Austrolestes) minutus n.sp.

Figs 20–22

Material examined. HOLOTYPE: male of 2.2 mm, Northwest Shelf, Western Australia, 19°04.8'S 118°50.7'E, 84 m, sand with ca. 10% gravel and some detritus, grab, 29 June 1983, CSIRO Fisheries, Stn 03/83/B5G, AM P44615. PARATYPE: Northwest Shelf, Western Australia, 19°05.3'S 118°54.0'E, 83 m, sand with ca. 10% gravel and some detritus, grab, 15 February 1983, CSIRO Fisheries, Stn 01/83/B4G, AM P44616 (1 male).

Diagnosis. *Austrolestes* with rostrum present in normal position. Cephalon along dorsal midline as long as pereonites 1 and 2 combined. Antenna 2 peduncle article 3 with proximal dorsomedial recurved robust seta.

Further description. Rostrum short, pointed, triangular. Antenna 1 longer than combined length of cephalon and pereon by about ½ pleon length, with up to 8 flagellar articles (left flagellum in holotype appears to be regenerating); peduncle article 1 with recurved robust seta ventrally in proximal half. Antenna 2 distinctly longer than cephalon and entire body combined; ventroapical projection of peduncle article 2 about 1½ times longer than wide, distally tapering with rounded apex carrying a few long setae.

Coxal plates 5 and 6 with posterior lobe poorly produced ventrally, posterior margin with rounded triangular projection. Pleonal side plates 1 and 2 evenly rounded.

Mandibular palp overreaching mandibular incisor with about ⅓ palp length, dorsolaterally with scattered acute microscales.

Fig. 20. *Ambicholestes (Austrolestes) minutus* n.sp., holotype. Scale bar: 0.5 mm.

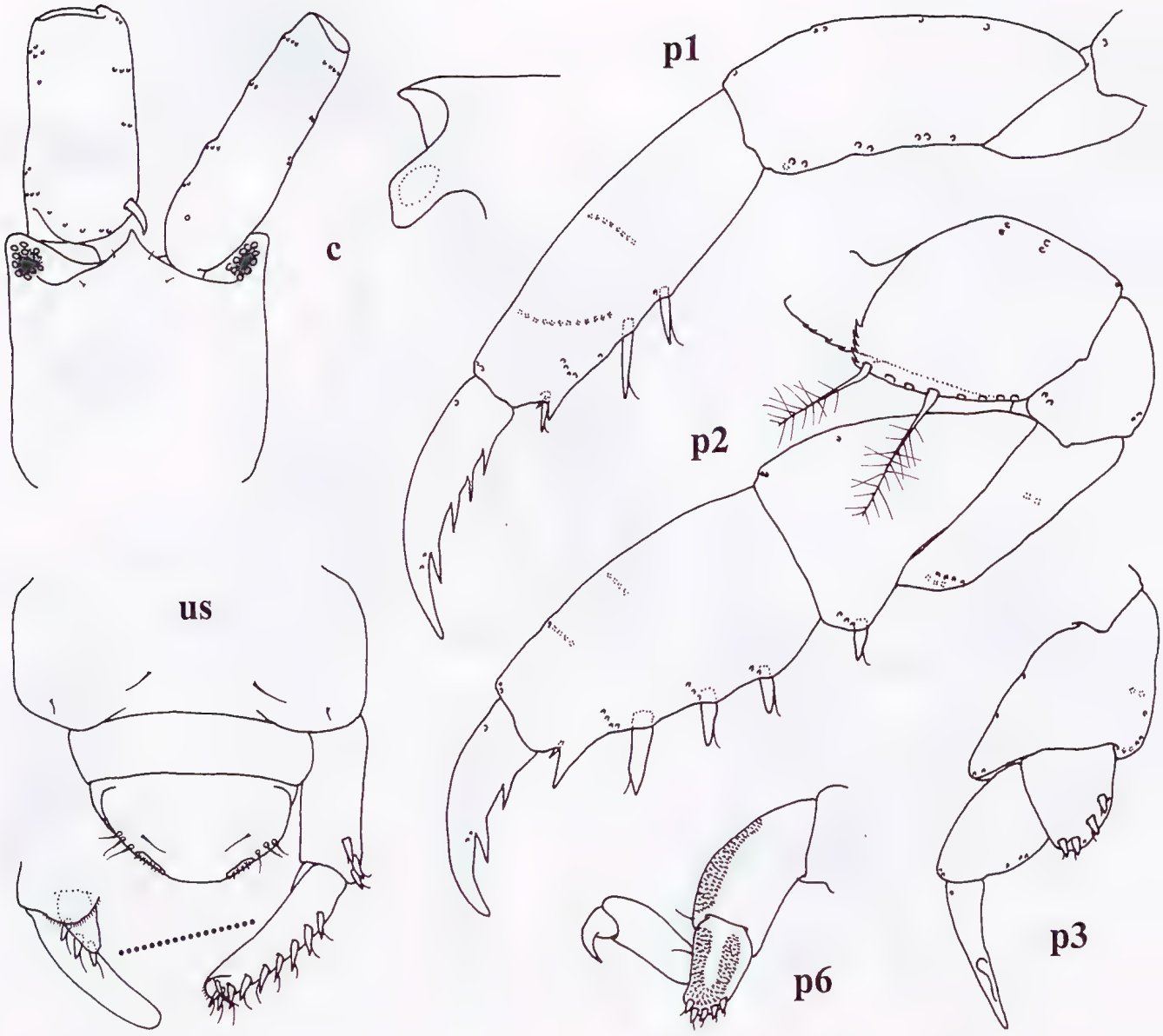

Fig. 21. *Ambicholestes (Austrolestes) minutus* n.sp., holotype. **c**, cephalon, dorsal and lateral view; **p**, pereopod (1, 2, 3 and 6); **us**, urosome, dorsal view, right uropod 1 in ventral view.

Pereopod 1 article 5 without posterior robust setae; article 6 with posterodistal tooth, 2 midposterior robust setae and 1 robust seta more distally. Pereopod 2 article 2 lateral anterior margin faintly convex, fringed with moderately long plumose setae with inflated bases, proximally with transverse row of small acute teeth, similar teeth present proximally on medial anterior margin; article 6 with 3 posterior robust setae. Pereopods 5 and 6 article 2 anteriorly with 1 long and 1 or 2 short setae, article 5 with up to 6 short robust setae in crescent.

Uropod 1 peduncle about $2^1/_3$ times longer than wide, with 2 or 3 distal robust setae; outer ramus about $3^1/_2$ times longer than wide, with single lateral row of up to 8 robust setae; inner ramus about $^2/_5$ length of outer ramus, distally tapering with 3 lateral to apical robust setae.

Urosomites 1 and 2 free. Urosomite 3 and telson dorsally fused.

Size. Largest male: 2.2 mm; (female not known).

Colour. Not known.

Biology. Not known.

Distribution. Western Australia, Northwest Shelf; 83–84 m depth.

Etymology. The specific epithet refers to the small size of the species compared with the other species in the subgenus.

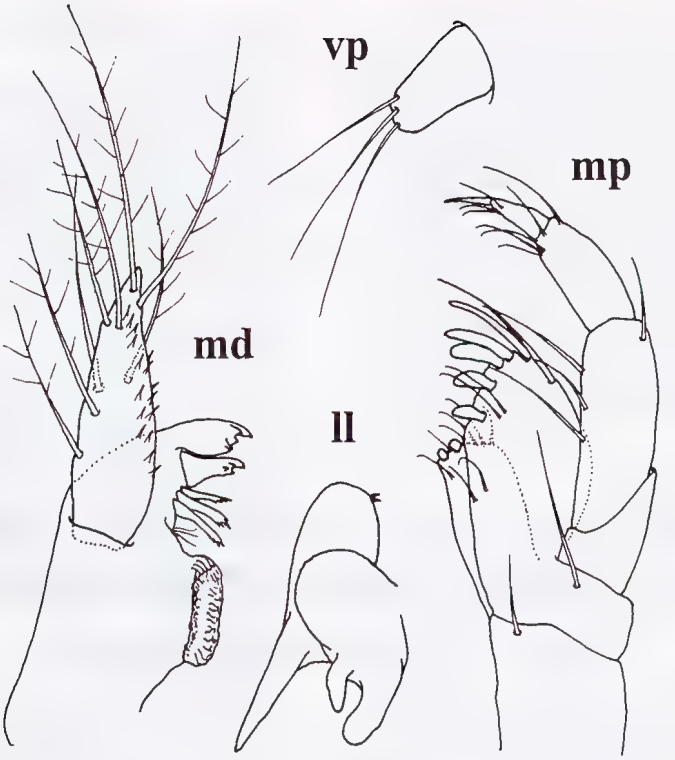

Fig. 22. *Ambicholestes (Austrolestes) minutus* n.sp., holotype. **ll**, lower lip; **md**, mandible; **mp**, maxilliped; **vp**, ventral process of article 2, antenna 2.

Table 1. Summary of diagnostic differences between *Caribboecetes* Just, 1983 and *Ambicholestes* n.gen.

	Caribboecetes	*Ambicholestes*	
		(Ambicholestes)	*(Austrolestes)*
Lower lip complex (C), simple (S)	S	C	C
Pereopod 7, article 7 with row of lateral setae (L), smooth (S)	S	L	L
Eyelobes inflated (I), not inflated (N)	N	I	I
Antenna 1 peduncle: article 1 shorter (S) or longer (L) that 2	L	S	S
Mandibular palp rounded with small 2nd article (R) or 1-articulate, pointed (P)	R	R	P
Male antenna 2 shorter (S) or longer (L) than cephalon plus pereon	S	S	L

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A Description of the Early Juvenile Colour Patterns of Eleven *Lethrinus* Species (Pisces: Lethrinidae) from the Great Barrier Reef, Australia

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ABSTRACT. The early post-settlement diurnal colour patterns of 11 of the 17 *Lethrinus* species presently known from the Great Barrier Reef are described: *Lethrinus atkinsoni* Seale; *Lethrinus erythracanthus* Valenciennes; *Lethrinus genivittatus* Valenciennes; *Lethrinus harak* Forsskål; *Lethrinus lentjan* Lacépède; *Lethrinus nebulosus* (Forsskål); *Lethrinus obsoletus* (Forsskål); *Lethrinus olivaceus* Valenciennes; *Lethrinus ornatus* Valenciennes; *Lethrinus variegatus* Valenciennes and *Lethrinus xanthochilus* Klunzinger. Where possible, descriptions cover the ontogenetic development of colour patterns from settlement through to attainment of the adult colouration. In addition, notes are provided on the pigmentation patterns of the late pre-settlement stage of *L. atkinsoni, L. genivittatus* and *L. variegatus*. Descriptions are based on field and aquarium observations and freshly collected specimens, with details of colour patterns retained by preserved material also included. The study is aimed as a guide to the identification of *Lethrinus* early juveniles, based primarily on colour patterns, with notes given on ecology and field identification. Morphological information is provided to facilitate the identification of early juveniles. Two new characters, cheek scales and maxillary serrations, are used to distinguish among recently-settled *Lethrinus* species. Juvenile lethrinids possess a complex range of colour patterns during their early juvenile period. Three general patterns are displayed by most species, based on stripes and irregular bands. These patterns and their rapid interchanges are described, and interpreted in relation to behavioural observations. Possible functions of the shared colour patterns are discussed in relation to the ecology of *Lethrinus* juveniles.

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The emperors (family Lethrinidae, *Lethrinus* species) are conspicuous percoid fishes found predominantly within coral reef habitats of the subtropical and tropical Indo-Pacific (Johnson, 1980; Springer, 1982; Carpenter & Allen, 1989). They often form an important component of reef-based fisheries throughout their range (Craik, 1981; Dalzell, 1988; Carpenter & Allen, 1989; Dalzell *et al.*, 1992; Jennings & Polunin, 1995), and are of considerable management interest. Fishes on coral reefs represent an increasingly exploited fisheries resource (Russ, 1991;

Johannes & Riepen, 1995), and a need exists to collect appropriate life history information for future stock assessment and management. However, a better understanding of the dynamics of these multi-species stocks will not be achieved without the ability to accurately identify the component species.

The importance of the early post-settlement period to the subsequent dynamics of reef fish populations has been increasingly recognised over the past decade (Doherty & Williams, 1988; Jones, 1991). However, information on these systems has mostly arisen from studies of sedentary taxa such as pomacentrids (damselfishes). Highly mobile species, and those which do not associate with the isolated coralline structures often employed in recruitment studies, have received scant attention. These taxa embrace some of the most valuable fisheries on Indo-Pacific coral reefs, yet knowledge of their early life histories is almost non-existent.

Lethrinus species comprise an ideal assemblage for examining early life history in exploited species, owing to their large size at settlement (Brothers *et al.*, 1983; Leis & Rennis, 1983; author's unpublished data) and ease of capture using conventional and recently-developed techniques (Doherty, 1987; Thorrold, 1992; Wilson, in prep.). Despite the prominence of the genus on Indo-Pacific coral reefs (Carpenter & Allen, 1989; Myers, 1989; Randall *et al.*, 1990), the juvenile stages have been largely unstudied. The development of suitable taxonomic criteria for distinguishing these individuals is a crucial step in redressing this imbalance.

Taxonomic studies of juveniles need to consider the extent of ontogenetic changes in body form and colouration. The external adult morphology of many *Lethrinus* species is very similar, but the degree of interspecific overlap is even greater in juveniles. Moreover, most morphological characters vary considerably during early ontogeny. By contrast, although *Lethrinus* juveniles are capable of rapid switches between alternative colour patterns (Smith, 1959), each of these alternate patterns varies little throughout the juvenile period, and characteristic colouration is easily distinguished in the field. Detailed descriptions of colour patterns therefore represent a valuable taxonomic tool for investigating juvenile assemblages.

The most recent revision of the Lethrinidae (Carpenter & Allen, 1989) provided brief descriptions of the adult colouration of the 28 *Lethrinus* species currently recognised. In addition, the typical juvenile colouration of *L. erythracanthus* and *L. nebulosus* was also figured. Juveniles of eight species are figured elsewhere (Wheeler, 1961; Allen & Swainston, 1988; Myers, 1989; Randall *et al.*, 1990; Shao *et al.*, 1992; Kuiter, 1992, 1993, 1996; Lee, 1993; Kuiter & Debelius, 1994; Lieske & Myers, 1994; Masuda & Kobayashi, 1994), although primarily in reference to mid or late-juvenile stages. Juvenile colour patterns of the remaining 20 species have not been reported.

The present study describes the early-juvenile stage of 11 of the 17 *Lethrinus* species recorded from the Great Barrier Reef region (Carpenter & Allen, 1989; D.McB. Williams, pers. comm.). Juveniles of the remaining six species—*L. laticaudis* Alleyne & Macleay, *L. microdon* Valenciennes, *L. miniatus* (Schneider), *L. rubrioperculatus* Sato, *L. semicinctus* Valenciennes and *Lethrinus* sp. 2 (undescribed species: Carpenter & Allen, 1989)—were not knowingly observed in the field. Collections and observations concentrated on a single locality on the Great Barrier Reef, although most of the species occur throughout the Indo-West Pacific or south-east Asia. Species designations follow those of Carpenter & Allen (1989).

This study is aimed as a guide to the field identification of living and freshly collected juveniles, based on colour patterns. Additional morphological information is also provided to facilitate the separation of similar species and the identification of preserved material. Descriptions focus on the identification of early post-settlement specimens, although notes are also included on distinguishing the late pre-settlement stage of three of the 11 species. Where possible, details are given of any changes in colouration occurring throughout juvenile ontogeny. Rapid switches among diurnal colour patterns are described from field and aquarium observations, and discussed in relation to behaviour and ecology.

Materials and methods

The main study and collection areas were located within the shallow lagoon surrounding Green Island (16°45'S 145°57'E), a small mid-shelf coral cay, 26 km from the mainland and a similar distance from the outer perimeter of the Great Barrier Reef. Additional observations were made in shallow, subtidal areas at Lizard Island (northern Great Barrier Reef, 14°40'S 145°28'E), Magnetic Island (Townsville, 19°15'S 146°50'E), and two localities (Bali [8°20'S 115°28'E] and Flores [8°32'S 122°13'E]) within the eastern Indonesian archipelago. The study period extended from August 1990 to November 1994, with field work concentrated around the November to February period of peak settlement (Russell *et al.*, 1977; Milicich, 1988).

The majority of specimens were collected using a small beach-seine net, 15×1.5 m, constructed from 9.5 mm nylon mesh. A 1 m cod-end in the net's centre facilitated the collection of small specimens. Because of the relatively large size at which *Lethrinus* individuals settle out of the plankton (Brothers *et al.*, 1983; Leis & Rennis, 1983; author's unpublished data), post-settlement juveniles of all developmental stages could be collected using this technique. In addition, late pre-settlement individuals, 14–21 mm, were sampled from around submerged fluorescent lights along the shoreline using a 6×1.5 m beach-seine net of 1 mm mesh. Specimens were killed by cold shock, and fixed in 10% formalin and preserved in 70% alcohol. A number of individuals were also kept alive in aquaria for periods of up to eight months to monitor ontogenetic changes in their colouration.

Photographic records were taken of both alive and freshly-killed specimens in a vertical aquarium. Fish to be photographed dead were killed by cold shock, and their fins set in an extended position using 40% formaldehyde.

Formalin was also brushed over the side of the body to be photographed in order to arrest any *post-mortem* fading of melanophore pigmentation.

In the present study, settlement refers to the transition between the pelagic and demersal phases of the life cycle. In the *Lethrinus* species considered here, known sizes at settlement range from 16 to 21 mm (Brothers *et al.*, 1983; author's unpublished data). Juveniles are the life cycle phase from the time of settlement to the onset of sexual maturity. However, *Lethrinus* species attain the adult colouration relatively early in comparison with other groups of reef-associated fishes such as the scarids and labrids (e.g., Bellwood & Choat, 1989). As such, the scope of the present study covers the size range from settlement to attainment of the adult colouration; this having occurred by 60 mm in most species. *Lethrinus* adult colour patterns are described and figured in Carpenter & Allen (1989) and are not referred to in any detail here. Unless otherwise noted, all lengths refer to the standard length (**SL**), the straight-line distance between the tip of the snout and the posterior edge of the hypural plate.

Colour information is provided as a basis for identifying field, captive and freshly-killed specimens, as well as preserved material. Horizontal, longitudinal markings are referred to as stripes. Where relevant, stripes are further designated as either dorsal, orbital, pectoral or ventral. Near-vertical, oblique and irregular markings are termed bands. Blotches refer to distinct cuboidal or circular markings. Pale areas between stripes, blotches and bands are referred to as interspaces. "Diagnostic colour notes" summarise the main diagnostic or characteristic features of a species' colour patterns. "Diagnosis" sections list the morphological features of greatest value for confirming colour-based identifications. "Colour in alcohol" descriptions were based on specimens collected during the present study, fixed in 10% formalin and retained in 70% ethanol for at least three months.

Carpenter & Allen (1989) provide information on morphological characters useful for separating *Lethrinus* species, based primarily on adults. In the present study, eight of these morphometric measurements and five scale-count characters (Fig. 1) were examined for their use in separating *Lethrinus* species as juveniles. Ontogenetic variation in the morphometric characters was assessed using a principal component analysis (PCA). Individuals were placed into five size-classes: 15–29.9 mm, 30–49.9 mm, 50–69.9 mm, 70–89.9 mm, and "adults"; the latter class representing values given by Carpenter & Allen (1989). The five species included in the analysis were those for which replicate observations were available within each size class. Data analysed were character means for each size class. Characters displaying minimal ontogenetic variation were further analysed using a canonical discriminant analysis of their separation of the 11 species. This analysis was restricted to individuals of ≤ 60 mm. All morphological measurements were made under a stereo microscope fitted with a calibrated ocular micrometer.

Two additional morphologies, the presence of cheek scales and presence and mean number of serrations along the outer surface of the maxilla, were also examined for

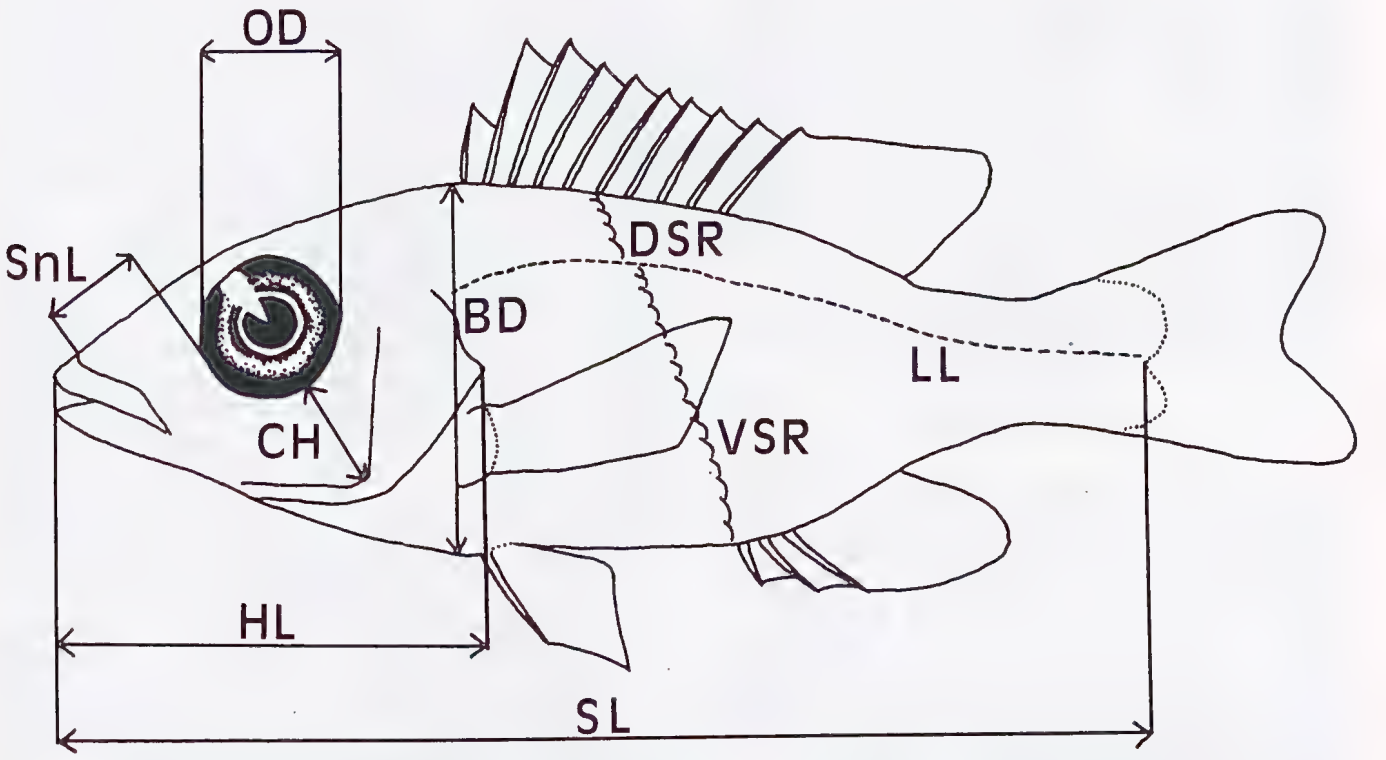

Fig. 1. Schematic summary of meristic counts and morphometric measurements examined in *Lethrinus* juveniles. Symbols: SL, standard length; BD, body depth; HL, head length; SnL, snout length; CH, cheek height; OD, orbit diameter; LL, number of lateral-line scales; DSR, number of dorsal scale rows; VSR, number of ventral scale rows.

separating *Lethrinus* species during the early post-settlement phase. Both characters have previously been discounted in the identification of *Lethrinus* species, although they have been used for distinguishing lethrinid genera (Sato, 1978; Carpenter & Allen, 1989).

Bibliographic information relating to early taxonomy is given in full in Carpenter & Allen (1989).

Voucher specimens were deposited in and specimens examined from the Australian Museum, Sydney (AMS); Museum of Victoria, Melbourne (NMV); and National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Juvenile distributions

Distribution patterns are only of limited use for separating early juveniles of the 11 species examined. At Green, Magnetic and Lizard Islands, *Lethrinus* juveniles occur almost solely over areas of shallow seagrass (≤ 7 m) until at least 80 mm. Furthermore, juvenile lethrinids typically co-occur in loose, multi-species schools. However, cross-shelf patterns in species composition are evident, with the number of species increasing from coastal areas outwards to mid-shelf reefs containing seagrass cover (Fig. 2).

At 80–90 mm, individuals of the common species (principally *L. atkinsoni, L. harak* and *L. obsoletus*) extend their distribution to include vegetated (e.g., *Sargassum* species) and unvegetated (sand, coral rubble, small patch reefs) habitats adjacent to seagrass beds. Other species, particularly *L. genivittatus, L. xanthochilus* and *L. variegatus*, migrate away from the seagrass habitat altogether at this size. With the exception of *L. harak*, few *Lethrinus* individuals greater than 120 mm reside within shallow habitats at Green Island (< 3 m). At this size, species such as *L. atkinsoni, L. lentjan, L. nebulosus, L. obsoletus* and *L. olivaceus* inhabit areas of soft substrate and patch reefs (5–15 m) surrounding the reef flat (line transect and beach-seine data in Wilson, in prep.; author's unpubl. obs.). Several species, particularly *L. genivittatus* and *L. variegatus*, frequent deeper interreefal habitats (data from otter trawls, T.J. Wassenberg, pers. comm.).

Further details of habitat-use by juveniles of individual species are given in the ecology sections below.

Colour patterns

The identification of juvenile lethrinids in the field was based primarily on colour patterns. Few *Lethrinus* species undergo marked ontogenetic changes in their juvenile colouration, and most can be readily identified from the time of settlement on the basis of diagnostic and characteristic patterns. Table 1 summarises the colour patterns of greatest value for distinguishing juveniles of the 11 *Lethrinus* species in the field and at capture. These patterns are also generally discernible in freshly-killed material and specimens maintained in aquaria.

Prior to settlement, body pigmentation in most *Lethrinus* species is restricted to yellow-orange xanthophores along the myosepta and as precursor markings to post-settlement patterns of stripes, blotches and bands. Sparse melanophores may also be visible over the body and spinous portion of the dorsal fin in some species. In late pre-settlement *L. atkinsoni, L. genivittatus* and *L. variegatus*, these form distinctive markings along the body, allowing individuals to be readily separated from other lethrinids. Following settlement, coloured stripes form rapidly from grey or tan melanophores in species such as *L. genivittatus, L. obsoletus* and *L. ornatus*. Darker body markings (e.g., bands along the dorsum) also begin to appear, although generally do not reach full intensity until individuals are 2–3 mm SL larger.

Three general colour patterns are found in most of the 11 *Lethrinus* species as early juveniles (Fig. 3), although interspecific differences exist in their intensity and form.

1—Primary stripes. Lethrinids may be placed into two groups based on the form and intensity of this pattern. The first group (*L. genivittatus*, Fig. 3A, Pl. 1E,F,G; *L. lentjan*, Pl. 2C; *L. obsoletus*, Pl. 2G; and *L. ornatus*, Pl. 3C) have pink to orange stripes. Four stripes are generally visible, hereafter referred to as the dorsal, orbital, pectoral and ventral stripes (Fig. 4; cf. Bellwood & Choat, 1989). Both the dorsal and orbital stripes originate behind the rear edge of the operculum and typically fuse near the caudal peduncle base. The dorsal stripe passes along the ventral margin of the lateral-line, while the orbital stripe extends from level with the lower half of the orbit. The pectoral stripe commences at the pectoral base and extends to midway along the caudal peduncle. The ventral stripe originates ventral to either the pectoral base (*L. lentjan* and *L. ornatus*) or medial dorsal spines (*L. genivittatus* and *L. obsoletus*), and passes along the lower flank to the ventral margin of the caudal peduncle. With the exception of *L. ornatus*, the dorsal stripe is seldom conspicuous, and may be obscured by overlying darker patterns (e.g., Pl. 1G). In *L. genivittatus* (Pl. 1E,F) and *L. obsoletus* (Pl. 2G), the ventral stripe is often similarly inconspicuous.

The second group comprises species possessing inconspicuous primary stripes (Fig. 3B). Clearest examples include *L. xanthochilus* (Fig. 3B; Pl. 3E), *L. erythracanthus* (Pl. 1D) and *L. nebulosus* (Pl. 2D). *Lethrinus xanthochilus* displays two irregular brown to grey stripes, generally in the pectoral and ventral positions. These typically originate on the operculum or adjacent to the pectoral base, and extend to above the second anal spine. Although inconspicuous in the field, they often intensify in response to capture or other disturbance. *Lethrinus erythracanthus* and *L. nebulosus* are exceptional within this category in displaying greater than four stripes, silver or pale blue, as a normal component of the diurnal field colouration.

Variation between the two groups is also evident in the ontogeny of their primary stripes. With the exception of *L. lentjan*, species from the first group display their stripes during both juvenile and adult phases. Species from the second group generally only retain their pattern until 60–80 mm (ca. 150 mm in *L. erythracanthus*), although *L. nebulosus* may display its primary stripes throughout the adult phase.

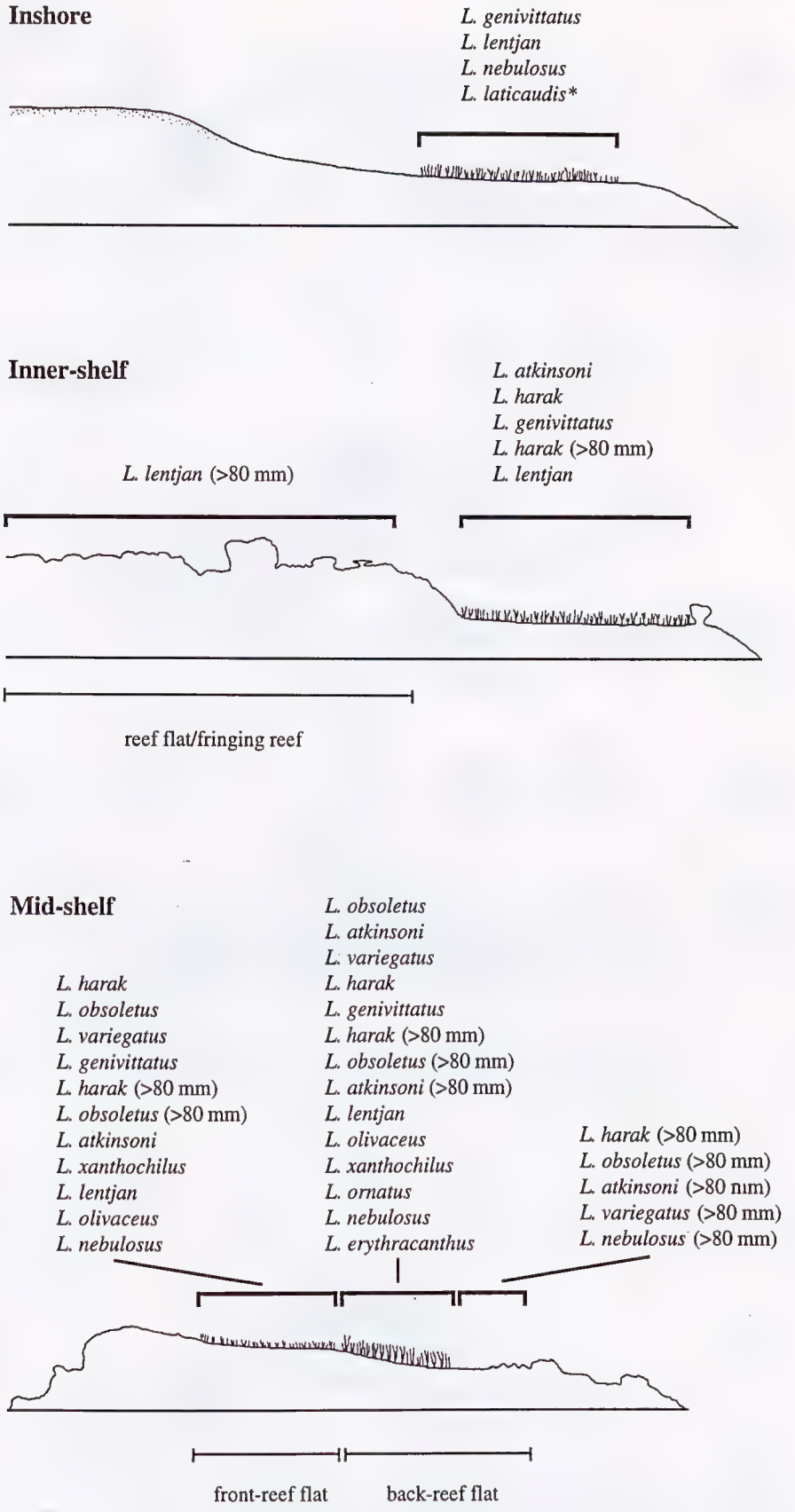

Fig. 2. General distribution patterns of *Lethrinus* juveniles within shallow habitats on the Great Barrier Reef. Species are listed in decreasing order of abundance and refer to the less than 80 mm size-class unless otherwise indicated. Based on observations from: Cleveland, Upstart and Princess Charlotte Bays (inshore); Magnetic Island (inner-shelf); Michaelmas Reef, Green and Lizard Islands (mid-shelf). Information from outer-shelf habitats was not available. Extent of seagrass cover indicated. *: not encountered during the present study, although common in the southern section of the Great Barrier Reef (I. Halliday, pers. comm.).

Table. 1. Characteristic and diagnostic colour patterns displayed by juvenile *Lethrinus* species 18–80 mm in the field and at capture. General forms of body and head colour patterns are given in Figs 3–5. †: body depth; ?: not known; *: identical colour to body background.

Character	*Lethrinus atkinsoni*	*Lethrinus erythracanthus*	*Lethrinus genivittatus*	*Lethrinus harak*	*Lethrinus lentjan*	*Lethrinus nebulosus*	*Lethrinus obsoletus*	*Lethrinus olivaceus*	*Lethrinus ornatus*	*Lethrinus variegatus*	*Lethrinus xanthochilus*
Primary stripes (Fig. 3A,B, 4)	2, usually absent, dark brown; interspaces off white	≥4, silver; interspaces yellow	3–4, golden orange to orange-tan; interspaces silver	absent	3–4, pale pink; interspaces off white	≥4, pale blue; interspaces yellow-tan	3–4, orange-tan; interspaces off white	absent	3–4, orange; interspaces silver	2, pale or absent, khaki; interspaces silvery off white	2, black-brown; interspaces silvery off white
Dark mid-lateral stripe (Fig. 3C)	width 4.0 in BD†	?	width 5.0 in BD	width 4.0 in BD	width 5.0 in BD	?	width 5.0 in BD	width 6.0 in BD	width 4.0 in BD	width 4.0 in BD	width 4.0 in BD
Banding (Fig. 3D)	frequent, dark brown to black	absent	frequent, black	frequent, black	frequent, pale to dark grey	frequent, pale to dark grey	frequent, black	frequent, black	rarely seen, pale to dark grey	rarely seen, pale grey	frequent, dark grey
Shoulder blotch (Fig. 3D, 5)	black, narrow vertical-rectangle	absent	black, silver halo, extending over lateral line	pale to dark grey, square, rarely seen	pale to dark grey, circle or vertical-rectangle	pale to dark grey, vertical-rectangle	grey to black, square or vertical-rectangle	black, horizontal-rectangle (Fig. 3D)	pale grey, square, rarely seen	pale grey, square, rarely seen	dark grey, square
Dorsal margin of lateral line	cryptic*	cryptic or with silvery dots	cryptic; rarely silver	cryptic	cryptic (< 31 mm) or with silvery dots	cryptic; occasionally with silvery dots	silvery cream	cryptic; rarely faded yellow-tan	cryptic	silvery cream	cryptic
Silvery mid-body interspace? (Fig. 3B)	no	no	no	no	no	no	no	no	no	no	yes (18–45 mm)
Suborbital markings (Fig. 3A,B)	none	none	2 tan bands at >35 mm	rarely dark triangle at >22 mm	rarely pale brown blotch at > 25 mm	rarely diffuse grey blotch at >38 mm	rarely 2 dark bands at >20 mm	single dark blotch at 40–60 mm	rarely broad diffuse brown blotch	single dark blotch at > 30 mm	single prominent dark blotch at 20–45 mm
Large rectangular blotch on mid-body? (Pl. 2B)	no	no	no	yes	no	no	no	no	no	no	no
Pelvic fin membrane	hyaline	hyaline or off white to pale grey	hyaline	hyaline	hyaline	off white to grey	hyaline	dark grey with underlying yellow to off white	hyaline	hyaline	dark grey with underlying yellow
Dorsal fin margin	hyaline or off white to pale scarlet	hyaline to dusky yellow	hyaline to off white	hyaline to greyish yellow or pale scarlet	hyaline or off white to pale maroon	hyaline to greyish yellow	hyaline or off white to pale pink	dark grey over yellow	hyaline or off white to pale scarlet	hyaline	hyaline to dark grey over yellow

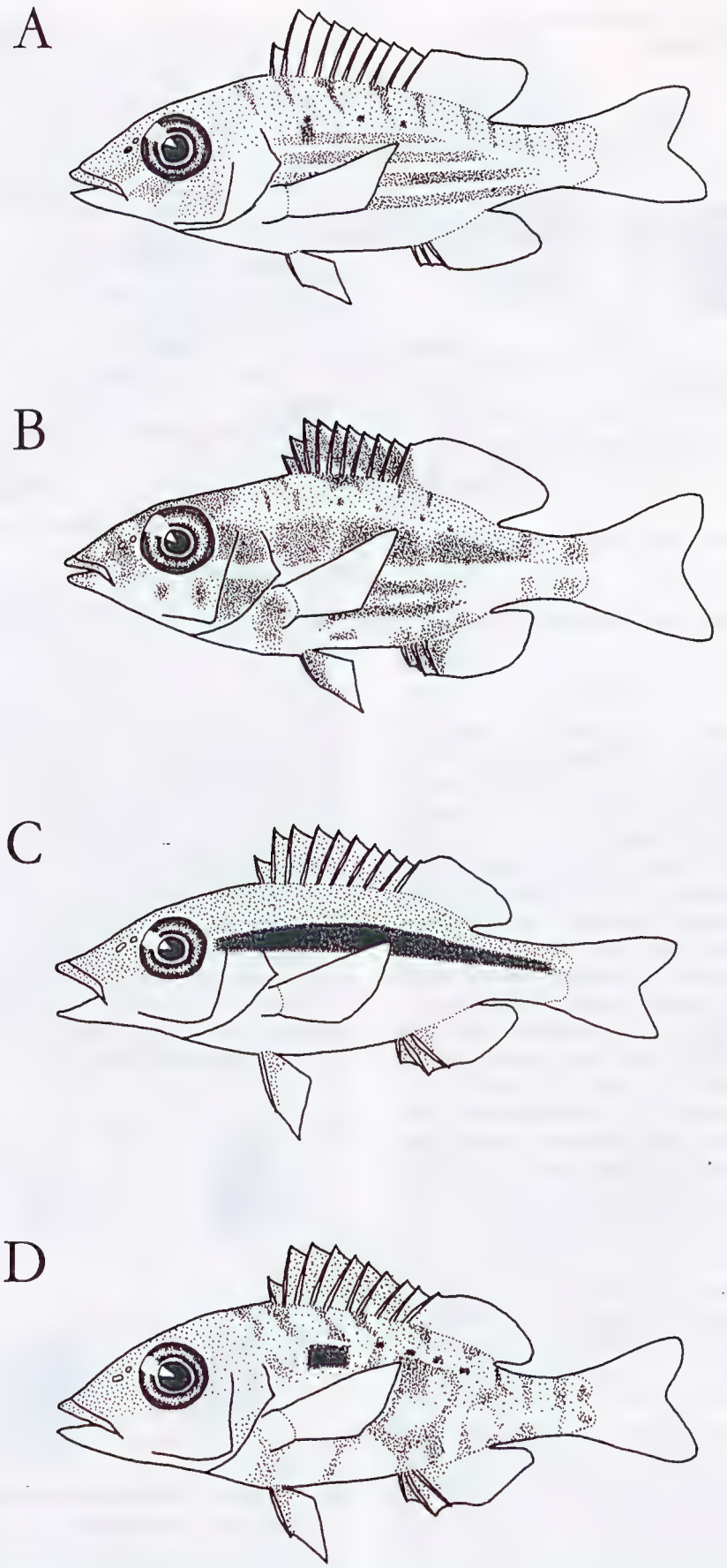

Fig. 3. General colour patterns displayed by *Lethrinus* juveniles: **A**—primary stripes-conspicuous form, based on *L. genivittatus* 25–80 mm SL; **B**—primary stripes-inconspicuous form, based on *L. xanthochilus* 25–45 mm SL; **C**—dark mid-lateral stripe, based on *L. olivaceus* 45 mm SL; **D**—dorsoventral banding, based on *L. olivaceus* 32–39 mm SL.

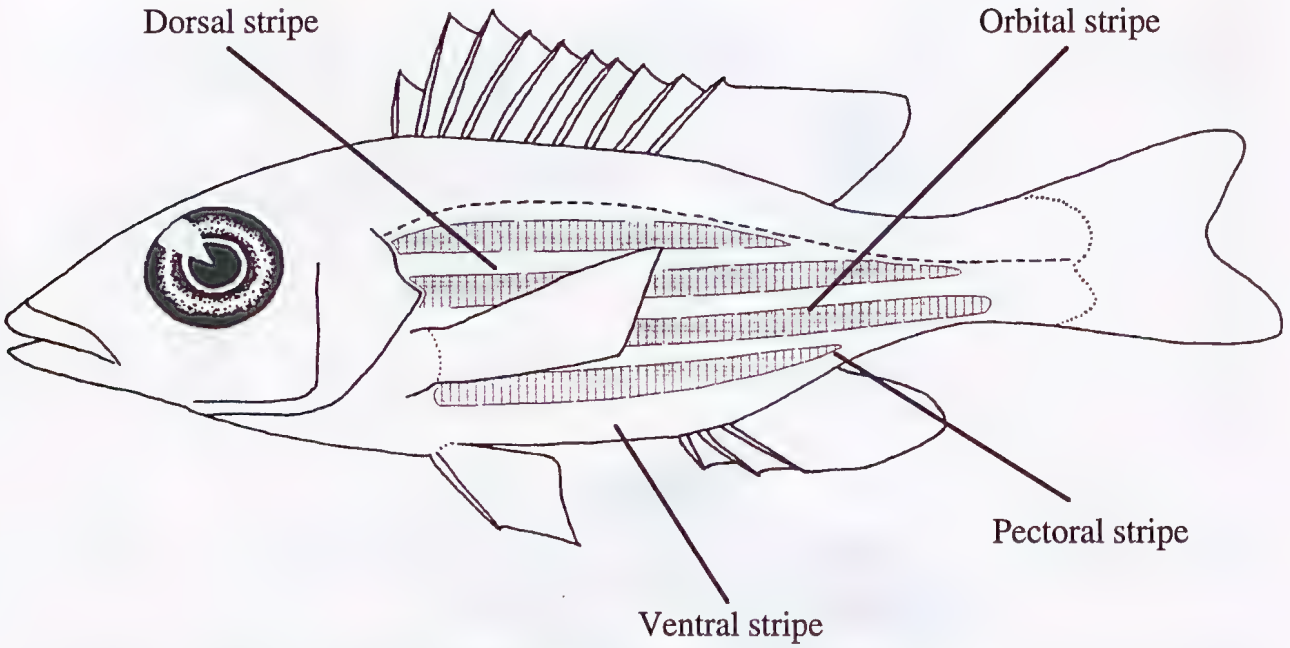

Fig. 4. Positioning and designation of the four primary stripes present in juveniles of numerous *Lethrinus* species.

2—Dark mid-lateral stripe. This pattern is only displayed in the field, and consists of a broad dark brown to black stripe originating along the rear margin of the orbit and terminating over the hypural plate (Fig. 3C; Pl. 1G; also Pl. 56E in Myers, 1989). Concomitant with its appearance is a partial or complete fading of other patterns. In *L. genivittatus* and *L. obsoletus*, a faded pectoral primary-stripe (rarely orbital, pectoral and ventral stripes together; as in Pl. 1G) may remain visible. Background colouration below the mid-lateral stripe is typically uniform, and paler than the dorsum. Field observations of early juvenile *L. erythracanthus* and *L. nebulosus* were too few to determine if a dark mid-lateral stripe pattern was present, although the remaining nine species do display this pattern.

Interspecific similarities in the dark mid-lateral stripe, and the associated fading of other diagnostic patterns, may lead to difficulties during field-identification. Differences in the relative breadth and/or intensity of the dark mid-lateral stripe may facilitate field diagnoses.

3—Banding. This colour pattern comprises dark bands and blotches along the length of the body (Fig. 3D). From 5–8 narrow grey to black bands appear along the dorsum, between the nape and base of the caudal peduncle (Pl. 1B,G, 2C,E,F). These either extend from the body margin to the lateral-line, or to halfway between, depending on the species and size of the individual. A further 2–3 bands appear along the caudal peduncle, usually connecting both body margins. Below the lateral-line, bands extend to the belly, either directly from the lateral-line and dorsal bands (as in Pl. 1A,B) or from a series of 3–4 dark blotches along the ventral lateral-line margin (Pl. 2E,F). In both forms, the bands are often linked in a network pattern, producing the *Lethrinus* "reticulated" appearance.

The ventral blotches, mostly cuboidal or rectangular in shape, extend along the body below the dorsal fin (as in Pl. 2C,E, 3D). The blotch, below dorsal spines 2–5 (5–7 in *L. olivaceus*), is generally the smallest and most intense, and designated as the "shoulder blotch". In species such as *L. atkinsoni*, this is the only blotch displayed (e.g., Pl. 1A,B).

The shoulder blotch displays some within-species variation, although its shape and intensity may nonetheless be diagnostic (Fig. 5). The shoulder blotch of species such as *L. obsoletus* varies from almost square to a deep rectangle. Shoulder blotches of this shape are round or square at settlement and deepen with ontogeny. *Lethrinus*

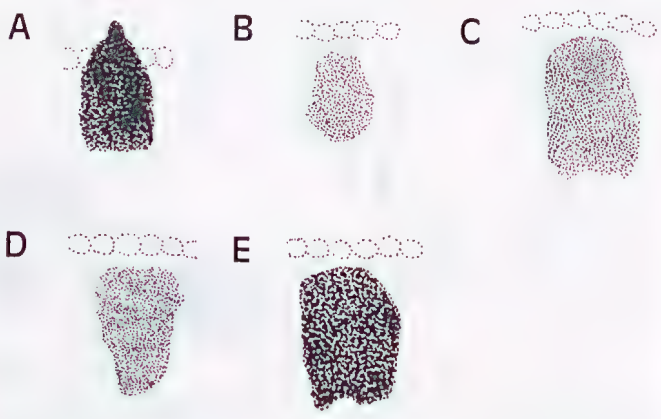

Fig. 5. Variations in the juvenile shoulder blotch pigmentation of selected *Lethrinus* species from the Great Barrier Reef. In species where two or more forms occur, underlined letters denote the predominant pattern(s) exhibited by freshly-killed specimens. Shoulder blotch positioning relative to the lateral-line scales is indicated. *Lethrinus genivittatus*—A; *L. lentjan*—B,C; *L. nebulosus*—C,D; *L. obsoletus*—B,C,E.

olivaceus is the only species with a horizontal shoulder blotch (Fig. 3D, Pl. 3A,B; Pl. 56E in Myers, 1989).

Banding is frequently displayed in the field, and also upon capture or death. In the field, species such as *L. atkinsoni, L. genivittatus* or *L. obsoletus* often display intense black banding over a uniform off-white background, obscuring other patterns (e.g., primary stripes). Banding in other species (particularly *L. ornatus* and *L. variegatus*) is generally inconspicuous or absent in the field, and only visible upon capture or after death. Both banding and mid-lateral stripe patterns are rapidly and frequently turned on or off at will, usually within 1–2 seconds. Observation of individuals displaying these patterns may be necessary for several minutes before diagnostic or characteristic colouration can be fully determined. In some cases, the collection of specimens for confirmation with meristic counts may be warranted.

Field observations

Display of the 3 shared colour patterns ("Colour patterns" above) appears strongly influenced by behaviour. Throughout the early juvenile period, lethrinids occur either as solitary individuals, or in loose schools with congenerics or species from several other families. Antagonistic interactions are most frequent between non-schooling individuals. When initially disturbed, banding (Fig. 3D) is rapidly displayed, often overlying a uniformly pale background. In all species intense displays of this nature are mainly limited to individuals of 30–50 mm. In small specimens (less than 30 mm), such displays are often restricted to appearance of the shoulder blotch.

Following initial display of the banding, primary stripes may become visible, particularly during flight from an aggressor. Often concomitant with the appearance of primary stripes is a partial fading of the banding. Prior to the appearance of primary stripes, field identification of some species (e.g., *L. genivittatus* and *L. obsoletus*) may be tenuous or impossible. However, field displays of the primary stripes are often less intense than those initiated at the time of capture, and collection of specimens for confirmatory identification may be necessary. In individuals larger than 50 mm, banding becomes progressively less prominent as a "fright colouration", and the increased clarity of the primary stripes or other characteristic colouration facilitates easier field identification.

During resting periods or when otherwise undisturbed, the dark mid-lateral stripe (Fig. 3C) is the most common pattern. Individuals switch it on while foraging among seagrass leaves or when hovering over the seagrass canopy (cf. Pl. 1G). Although most common when solitary, it may also be displayed by individuals swimming in relatively discrete schools. When disturbed, the dark mid-lateral stripe is rapidly replaced by either the primary stripes, dorsoventral banding, or a combination of the two. Upon removal of the cause of disturbance, the dark mid-lateral stripe is resumed. Solitary, resting individuals may also occasionally display an exceedingly faint pattern of primary stripes, without overlying dark markings.

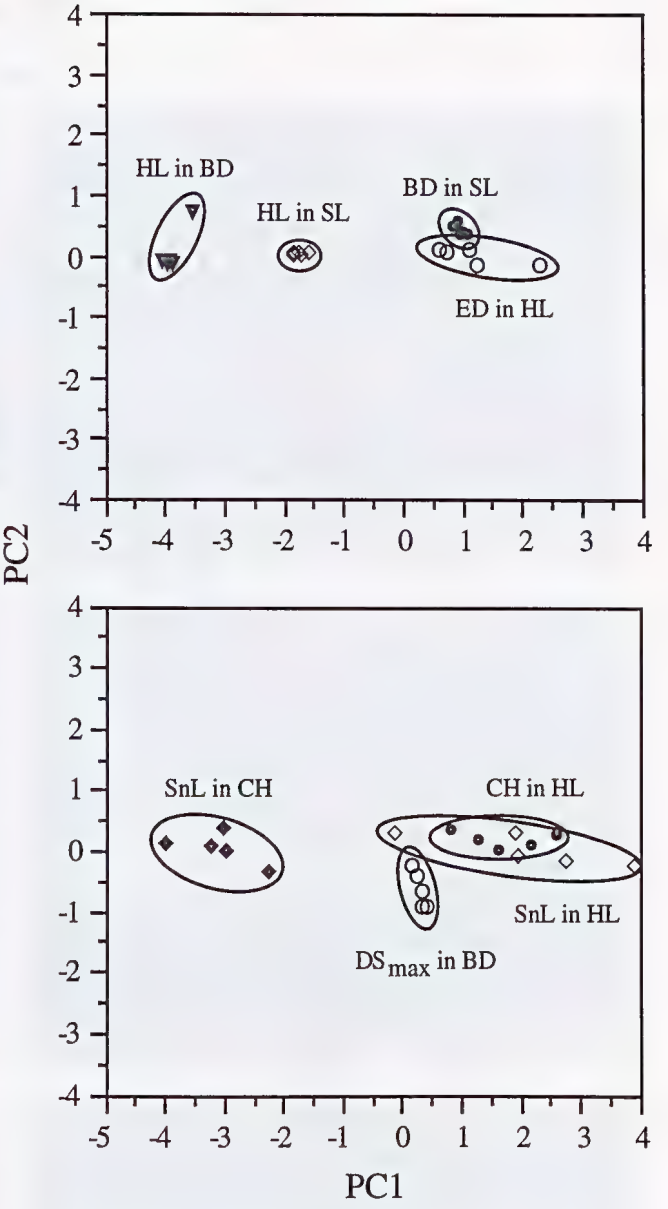

Fig. 6. Results of principal component analysis of ontogenetic variation in *Lethrinus* morphometric ratios. Analysed were five size-classes across *L. atkinsoni, L. genivittatus, L. harak, L. obsoletus* and *L. variegatus*. Principal components 1 and 2 were plotted, together accounting for 98.9% of variance in the data. Ontogenetic variation within a character was evidenced by an elongate ordination of size-class values along either axis (e.g., SnL in HL). Ratio symbols follow those detailed in Fig. 1, except for: DS_{max}, length of longest dorsal spine. For clarity, ratios 1–4 are shown separated from 5–8.

The dark mid-lateral stripe pattern of *Lethrinus* species is extremely similar to that of *Siganus fuscescens* (Pl. 10 G in Woodland, 1990). This may lead to difficulties in separating these taxa when recently-settled (25–30 mm). Both groups also display similar behaviours: swimming in short bursts, periodically hovering to pick small food items off seagrass leaves, and often schooling together. This association is addressed further in the Discussion.

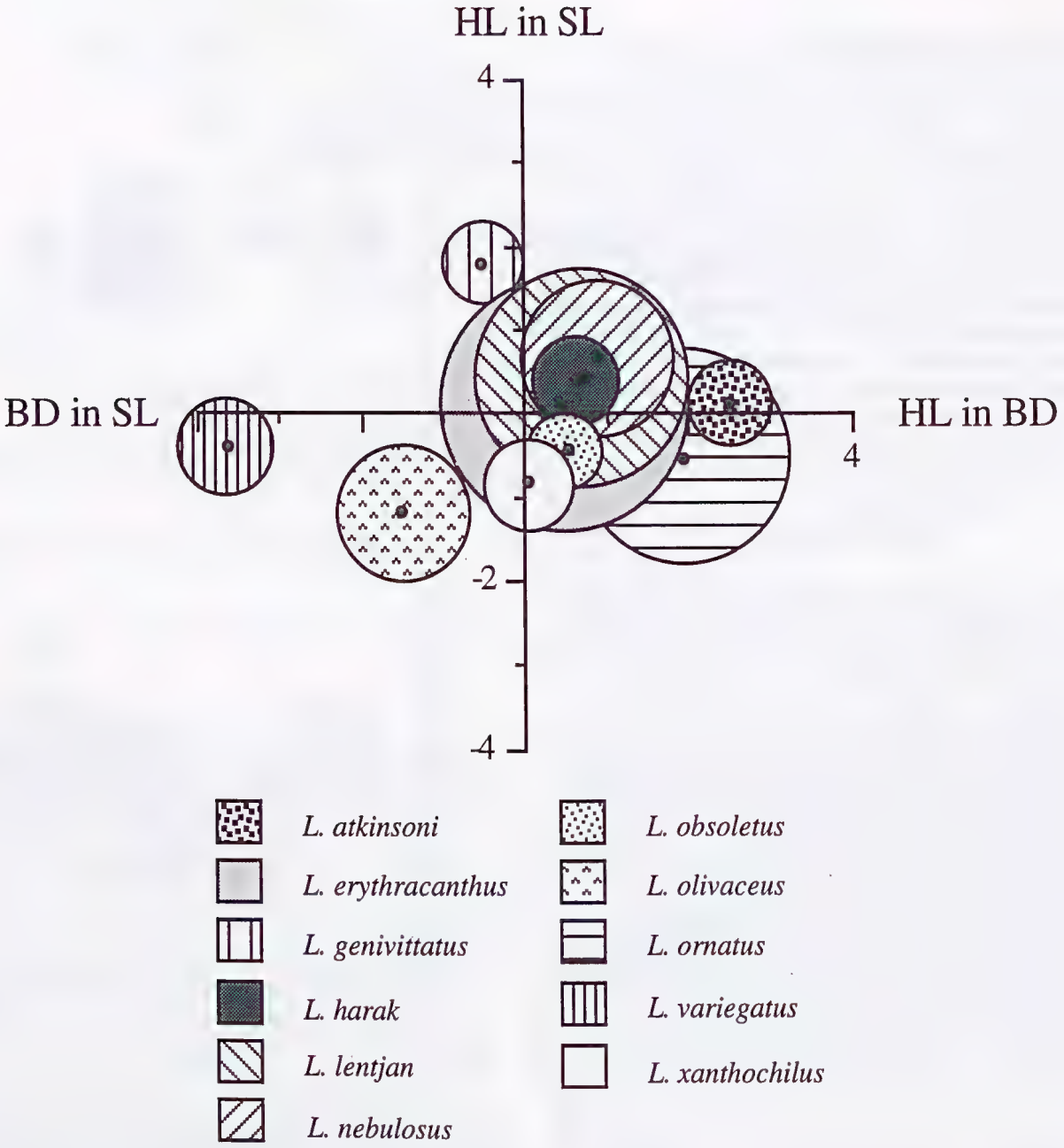

Fig. 7. Results of canonical discriminant analysis of relative body and head depths for the morphological separation of *Lethrinus* species as early-juveniles (≤ 60 mm). Canonical variates 1 and 2 are plotted; together, these account for 95% of variance in the data. The characters responsible for variation along each axis are shown. Circles surrounding species means represent 95% confidence ellipses.

The siganid pattern may be distinguished from that of *Lethrinus* species by the thin off-white border along both the dorsal and ventral margins of the mid-lateral stripe (cf. either a pale dorsal border in *L. obsoletus* and *L. variegatus* or no such pale borders in the remaining nine species described here). Juvenile siganids also possess a more ovoid body and rounded snout, with their eyes further from the head margin.

Morphological characters for distinguishing *Lethrinus* juveniles

Morphological characters may augment the colour-based identification of *Lethrinus* juveniles, particularly in preserved material where characteristic colour patterns are faded or absent. However, the application of "adult" characters (Carpenter & Allen, 1989) to the identification of juveniles must proceed cautiously. There are two principal reasons for this. Firstly, a substantial degree of allometric growth occurs during early post-settlement

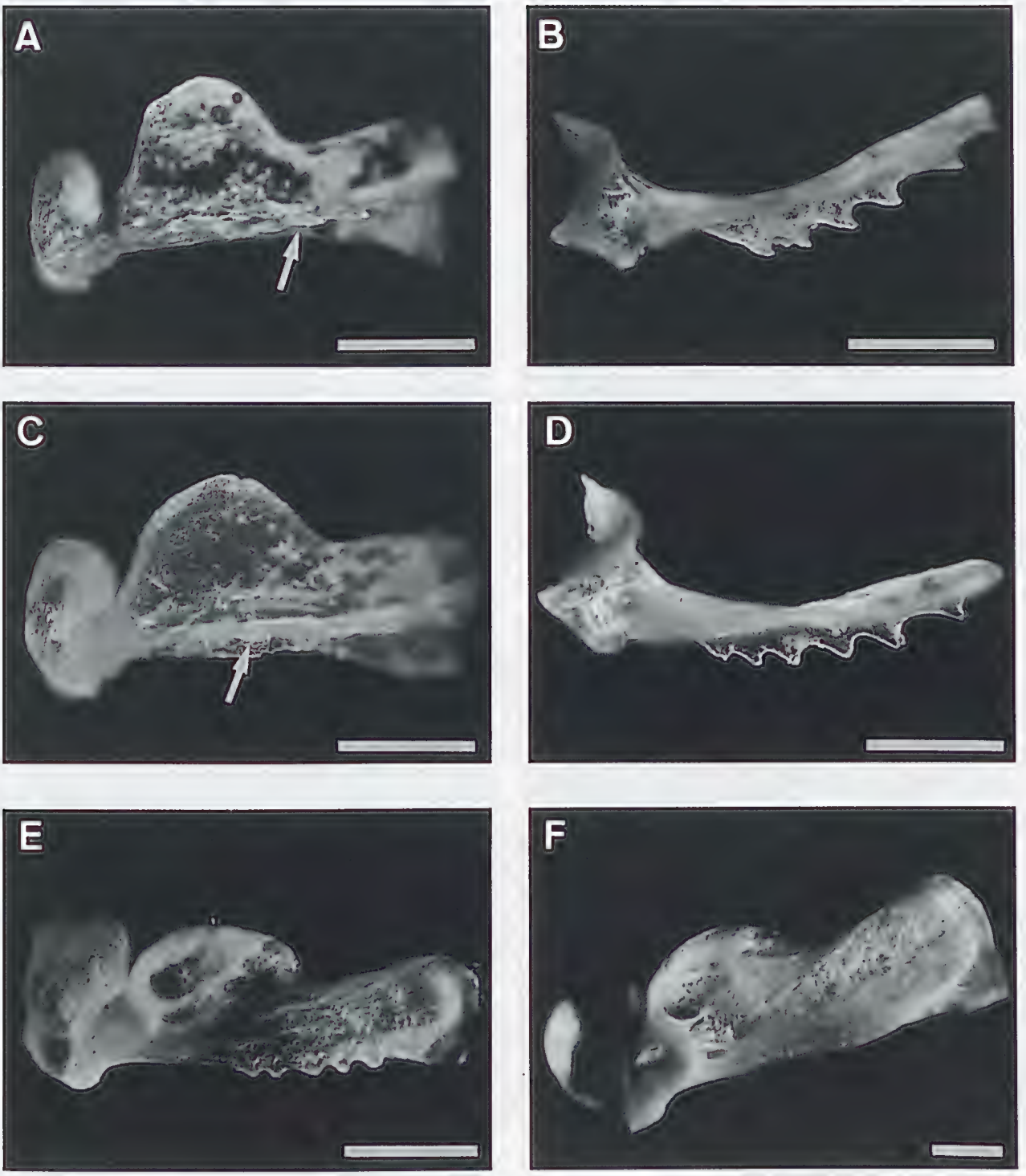

Fig. 8. Maxilla ontogeny in *Lethrinus genivittatus* juveniles, showing the occurrence of serrations along the left maxilla. A,B 18.9 mm SL (pre-settlement); **A**—oblique lateral view, **B**—dorsal view. **C,D**—21.4 mm SL (post-settlement); C: oblique lateral view, D: dorsal view. **E**—42.0 mm SL; lateral view. **F**—82.6 mm SL; lateral view. Serrations occur along a medial ridge in A and C (arrows) and absent in F. Scale bars = 0.5 mm (A–D) and 1 mm (E–F).

development, particularly in relation to growth of fin elements and protrusion of the snout. Secondly, this period of rapid structural change is characterised by highly variable intraspecific development trajectories.

The PCA of ontogenetic variation in the eight morphometric ratios identified trends along the first two axes (Fig. 6). Variation along these axes reflected ontogenetic changes in head shape (axis 1, 96.3% of total variance) and two body-depth ratios (axis 2, 2.6%). Five characters varied among size-classes, evidenced by their elongate elipses: orbit diameter in head length, snout length in head length, cheek height in head length, snout length in cheek height and length of longest dorsal spine in body depth. By contrast, the three remaining ratios (body depth in standard length, head length in standard length, head length in body depth) varied little with body size. The latter character did, however, vary between individuals of ≤ 89 mm and the "adult" size class.

Using these three ratios, a canonical discriminant analysis of morphological differences among the 11 species indicated a differentiation of body profiles along canonical axis 1 (Fig. 7). This showed a gradation from the slender-bodied *L. variegatus* through to deep-bodied *L. atkinsoni* and *L. ornatus*. Of the two characters responsible for variation along axis 1, body depth in standard length is the simplest to discern under field conditions. Values of this ratio for individual species are provided in the species descriptions below.

Three of the five scale-count characters (LL, DSR, VSR) did not vary ontogenetically, although they may be difficult to discern in specimens without full body pigmentation. Both the pectoral axil or parietal scales (see Carpenter & Allen, 1989) were found to be unreliable for identifying early juveniles. Parietal scales appear at around the time of settlement, although their number varies with both SL and side of the fish. Scales on the pectoral axil are entirely absent until 60–80 mm.

Both the cheek scales and serrations along the maxilla may further facilitate the identification of recently-settled specimens. A full complement of cheek scales is present in all lethrinids at settlement (Leis & Rennis, 1983). In *Lethrinus* species, they are lost shortly thereafter, with the mean size (SL) at which a species looses its scales useful as a diagnostic character. Cheek scales become difficult to detect as they recede towards the preopercular angle with increasing body size. Serrations along the outer edge of the maxilla (Fig. 8) are also present at settlement, although they are progressively lost soon thereafter in most species. In *L. genivittatus*, they may be present until 70–80 mm.

Lethrinus atkinsoni Seale

Pl. 1A,B,C

Material examined. (37 specimens: 18–126 mm). AUSTRALIA Great Barrier Reef region, AMS I.20578-003 (1:114 mm), AMS I.22674-007 (1:20 mm), AMS I.34147-003 (2:61–78 mm), AMS I.34323-042 (1:78 mm), AMS I.34911-001 (2:30–35 mm), AMS I.34912-001 (3:20–25 mm), AMS I.34912-002 (1:20 mm), AMS I.34912-003 (1:22 mm), AMS I.34913-001 (1:23 mm), AMS I.34913-002 (1:38 mm), USNM 336678 (2:20–21 mm), USNM 336679 (1:33 mm), USNM 336692 (1:31 mm), not retained (12:18–55 mm); INDONESIA Ceram, AMS I.18469-066 (2:40–45 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17099-049 (1:48 mm); SOLOMON ISLANDS New Georgia Island, AMS I.22128-153 (1:126 mm).

Diagnosis. Body relatively deep, depth 2.4–2.8 in SL; 4.5 dorsal scale rows, 14–15 ventral scale rows; maxillary serrations 3–5 (rarely 6) at 18–21 mm, 2–5 at 22–30 mm, absent at greater than 35 mm; cheek scales absent at greater than 29 mm; at 18–115 mm dorsal spine 4 or 5 the longest.

Diagnostic colour notes. Snout and dorsum yellow-tan; intermittent yellow hue along caudal peduncle and fin (at greater than 25 mm); 4 black bands below dorsal spines fusing mid-body into 2 pointed configurations (Pl. 1A,B); shoulder blotch narrow and vertical; width of dark mid-lateral stripe approximately 4.0 in body depth; no dark markings below orbit; fins hyaline.

Pre-settlement colour notes. At 18–20 mm: body translucent off-white, melanophore patterns overlying yellow-orange xanthophore pigmentation; banding and shoulder blotch near-identical to juveniles (Pl. 1A,B; "Colour notes" below) although less distinct and intense; dark markings on head restricted to scattered melanophores over brain and diagonal black band through orbit; fins hyaline.

Colour notes. A distinctive species, displaying several colour patterns, rapidly switching between them within 1–2 seconds, only subtle variation noted with ontogeny. At 18–80 mm: snout and nape yellow-tan, dorsum either yellow-tan (without dark bands), off-white (with banding, noted below) or pale grey-tan (freshly killed, Pl. 1B), cheek and flank off-white to pale grey-tan, belly off-white; cheek without dark markings, eye often bisected by near-vertical black band (Pl. 1B); fins mostly hyaline, anterior two thirds of spinous fins off-white, dark bands bordering dorsal fin extending onto basal half of fin, melanophores absent from inner pelvic rays, at greater than 25 mm caudal fin yellowish, hue extending in broad stripe along caudal peduncle to mid-body, usually faded during banding displays, outer margin of dorsal, anal and caudal fins often pale scarlet at greater than 50 mm (as in Masuda & Kobayashi, 1994, Pl. 7, p. 175).

Two dark intermittent patterns. (A) Banding: 8–9 sharply-defined dark brown to black bands originating along dorsal margin of body and caudal peduncle, most tapering mid-body, 2 bands between head and dorsal fin either terminating at lateral-line (Pl. 1A) or fusing at base of pectoral fin, 2 bands below dorsal spines fusing above belly, 4–5 bands between dorsal and caudal rays extending unfused to ventral body-margin; 2 ventral bands near anal-fin origin fusing mid-body and extending in pointed configuration to above lateral-line, occasionally appearing as single broad stripe; narrow vertical shoulder blotch below dorsal spines 3–4 (Pl. 1A,B,C), marginally darker

than adjacent bands. When stressed (Pl. 1C), body paler than when freshly collected, banding and shoulder blotch slightly broader and darker, medium brown blotches along snout and operculum. (B) Dark mid-lateral stripe: frequently displayed at 30–80 mm, medium brown, extending from orbit to base of caudal peduncle, width approximately 4.0 in body depth.

Colour in alcohol. At 18–55 mm, head and body uniform pale off-white tan, belly off-white; banding and shoulder blotch of variable intensity, usually dulled; fins hyaline, melanophores retained; at greater than 30 mm, subtle broad pale stripe sometimes present between caudal-fin origin and above pectoral-fin base.

Ecology. Common, settles into shallow dense seagrass cover on lagoonal or fringing coral reefs (0.2–6 m; *Cymodocea, Halodule, Thalassia*), an ontogenetic shift to adjacent reef-flat habitats apparent at 80–100 mm, thereafter seldom observed over seagrass; at 15–30 mm, remaining close to the seagrass canopy and rapidly seek cover therein when disturbed, larger individuals (30–80 mm) escape over the seagrass canopy; settlement recorded from 17–19 mm, small individuals (less than 40 mm) solitary, larger juveniles (40–80 mm) occasionally join small (approximately 10–20 individuals) schools with similarly-sized congeners (*L. genivittatus, L. harak* and *L. obsoletus*), *Lutjanus fulviflamma* (Lutjanidae), *Parupeneus indicus* and *P. barberinus* (Mullidae), *Stethojulis strigiventor* (Labridae), and in particular, *Siganus fuscescens* (Siganidae); juveniles forage diurnally over and between seagrass shoots, occasional brief aggressive interactions with congeners when recently-settled, noted resting on the substrate among seagrass shoots at night, not fleeing when approached.

Field identification. *Lethrinus atkinsoni* can be distinguished from other *Lethrinus* species by a combination of its deep body profile, characteristic dark banding, yellow caudal peduncle and fin (greater than 25 mm), and vertical shoulder blotch. Bellwood & Choat (1989) note the early-mid juvenile phase of the scarid *Hipposcarus longiceps* to mimic the behaviour, body shape and colouration of similarly-sized *Lethrinus* species. Juvenile *H. longiceps* with a yellow mid-lateral band (Pl. 1D, Bellwood & Choat, 1989) may be confused with *L. atkinsoni*, although the black dot at the base of the caudal rays in *H. longiceps* separates these species. Juvenile *L. atkinsoni*, 30–80 mm, frequently exhibit a dark mid-lateral stripe pattern, and form schools with juvenile *Siganus fuscescens* displaying a near-identical pattern. When approached, *L. atkinsoni* juveniles usually revert to their distinctive banding (Pl. 1A,B) or yellow caudal-stripe patterns. The yellow-tan body of small *Siganus doliatus* (22–25 mm) may lead to confusion with *L. atkinsoni*, although the banding and pointed snout of *L. atkinsoni* readily separates these species.

Previous descriptions. Juvenile *L. atkinsoni* of unknown size were figured by Allen & Swainston (1988) and Shao *et al.* (1992). Masuda & Kobayashi (1994) included a colour plate of a specimen 75 mm total length, displaying the characteristic yellow caudal stripe and dark banding.

Lethrinus erythracanthus Valenciennes

Pl. 1D

Material examined. (3 specimens: 25–26 mm). AUSTRALIA Great Barrier Reef region, AMS I.34914-001 (1:25 mm), AMS I.34914-002 (1:26 mm), USNM 336680 (1:25 mm).

Diagnosis. At 25–26 mm, body moderately deep, depth 2.8–2.9 in SL; 4.5 dorsal scale rows, 16 ventral scale rows; maxillary serrations 4–5; cheek scales present; dorsal spine 3 or 4 the longest.

Diagnostic colour notes. At 25–26 mm, dorsum and flanks yellow-orange, belly off-white yellow; 4 narrow silver primary stripes (4–6 at 50–100 mm, Pl. 1D), broad interspaces yellow-orange; no dark markings on body or cheeks; fins hyaline (but see "Identification note" below).

Colour notes. A species characterised by marked colour changes throughout life history, although little ontogenetic variation apparent during early post-settlement phase; no rapid colour pattern changes. At 25–26 mm, freshly collected: dorsum deep yellow-orange, fading to pale orange belly, no dark banding or mid-lateral stripe patterns, silver peritoneal lining faintly visible; 4 narrow silver stripes below lateral-line, originating behind operculum and pectoral fin base, orbital stripe extending to base of caudal rays, other stripes terminating near base of caudal peduncle, interspaces broader than stripes and of similar colouration to rest of body; cheek and operculum off-white to silver, no dark markings, snout and lips grey to pale yellow-orange, nape slightly reddish; fins hyaline, spinous fins with moderately-dense melanophores, yellow tinge distally, inner pelvic membranes without dense melanophores (but see "Identification note" below).

At 50–80 mm, in field (Pl. 1D): body yellow-orange, dorsal scales pale-centred, lateral-line denoted by row of silver dots, head yellowish grey; pectoral fins hyaline, caudal, dorsal and anal fins dusky yellow, fading posteriorly, pelvic fins off-white; 5–8 narrow silver stripes along flanks, medial stripe of greatest intensity, extending from lower margin of orbit to base of caudal rays, remaining stripes running from operculum to base of caudal peduncle.

Colour in alcohol. At 25–26 mm, head and body uniform off-white yellow, peritoneum off-white; silver primary stripes inconspicuous, initially darker than surrounding body, faded after ca. 2 years; fins hyaline, melanophores retained.

Ecology. Settlement and nursery sites unknown, rare at Green Island, three recently-settled specimens were collected from a sheltered seagrass bed (0.5–2.0 m; *Cymodocea* and *Thalassia*) adjacent to the shoreline; field behaviours unknown.

Field identification. Early-juvenile *L. erythracanthus*

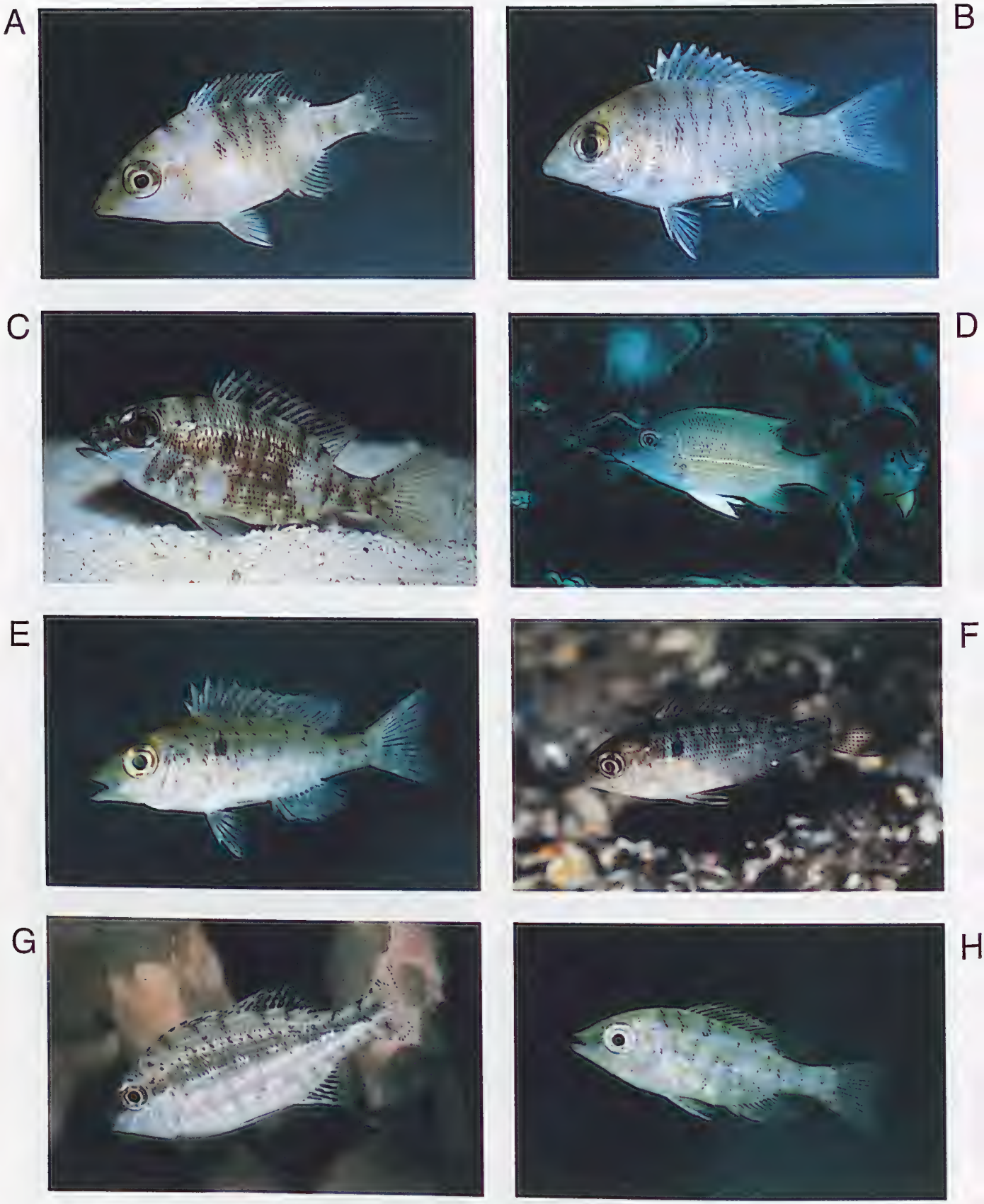

Plate 1. **A**—*Lethrinus atkinsoni*, 23 mm SL, AMS I.34915-001, live, Green Island. **B**—*Lethrinus atkinsoni*, 23 mm SL, AMS I.34915-001, dead, Green Island. **C**—*Lethrinus atkinsoni*, 50 mm SL, live (stress colouration), Green Island. **D**—*Lethrinus erythracanthus*, 80 mm SL, underwater photograph by R.H. Kuiter, Flores (Indonesia). **E**—*Lethrinus genivittatus*, 30 mm SL, AMS I.34919-001, dead, Green Island. **F**—*Lethrinus genivittatus*, approx. 30 mm SL, underwater photograph by R.H. Kuiter, Sydney Harbour. **G**—*Lethrinus genivittatus*, approx. 40 mm SL, underwater photograph by R.H. Kuiter, Sydney Harbour. **H**—*Lethrinus harak*, 20 mm SL, AMS I.34920-002, live, Green Island.

individuals are rarely encountered in the field; no underwater observations were made during the present study. At the size examined, *L. erythracanthus* field colouration could be confused with both *L. genivittatus* and *L. atkinsoni* juveniles of a similar size. All three species may be yellow-orange over at least the snout and dorsum. The lack of dark intermittent patterns in *L. erythracanthus* may distinguish it from other species.

Identification note. The density of pigmentation on the innermost pelvic membranes varies among *L. erythracanthus* individuals (Carpenter & Allen, 1989). In the specimens examined, this ranged from a faint covering of fine melanophores to absence. Although the small sample and narrow size range did not allow ontogenetic effects to be distinguished from variation at the individual or population level, this character may be useful for separating *L. erythracanthus* from other lethrinid juveniles.

Previous descriptions. The *L. erythracanthus* juvenile stage has been figured by Carpenter & Allen (1989; length not given) and Lieske & Myers (1994; length not given), and colour plates included in Myers (1989; 150 mm), Randall *et al.* (1990; length not given), Kuiter (1992; 80 mm, reproduced here in Pl. 1D) and Masuda & Kobayashi (1994, 50 mm total length).

Lethrinus genivittatus Valenciennes

Pl. 1E,F,G, Figs 3A, 5A, 8, 9

Material examined. (38 specimens: 17–99 mm). AUSTRALIA New South Wales, AMS I.17458-004 (1:32 mm), AMS I.26438-003 (4:17–34 mm), AMS I.30814-007 (1:25 mm); Great Barrier Reef region, AMS I.20786-012 (3:18–23 mm), AMS I.32476-003 (2:18–19 mm), AMS I.34911-002 (7:20–26 mm), AMS I.34911-003 (1:39 mm), AMS I.34911-004 (1:25 mm), AMS I.34915-001 (2:18–21 mm), AMS I.34916-001 (1:19 mm), AMS I.34917-001 (1:31 mm), AMS I.34917-002 (1:19 mm), AMS I.34919-001 (1:30 mm), AMS (I.33287-001) (1:20 mm), USNM 336681 (6:21–32 mm); Queensland south of Great Barrier Reef, AMS IB.1023 (4:46–70 mm), AMS E.1359 (1:99 mm).

Diagnosis. Body depth variable, 2.6–3.8 in SL, deepening with increased SL; 4.5 dorsal scale rows, 15 (rarely 16) ventral scale rows; maxillary serrations 5–7 (occasionally 4) at 16–40 mm, fewer at greater than 40 mm, absent by 80–90 mm; cheek scales retained until 25–27 mm; dorsal spine 2 relatively elongate, its length ≥ dorsal spine 3 at greater than 30–35 mm (occasionally 25–30 mm).

Diagnostic colour notes. Dorsum yellow-tan, 4–6 distinct narrow black bands extending to lateral-line, body off-white tan to silver ventrally; intense cuboidal shoulder blotch, surrounded by silvery halo (Pl. 1F), pointed tip crossing lateral-line (Fig. 5A); 3–4 orange stripes below lateral-line, of equal intensity and width, interspaces silver; at greater than 35 mm, 3 broad tan bands on suborbit and preoperculum (Pl. 1G); fins hyaline.

Pre-settlement colour notes. Pre-settlement pigmentation variable with SL (16–21 mm), complete by 22 mm (Fig. 9): dorsum and flank translucent off-white to pale tan, belly and cheek silver; prior to appearance of melanophores, pigmentation restricted to yellow-orange xanthophores along myosepta and horizontal septum, sparse melanophores first appear over caudal peduncle and 1–3 scales below dorsal spines 4–5 forming early shoulder blotch (Fig. 9A), later increasing to 4–6 scales; 3–4 cuboidal blotches appearing between lateral-line and horizontal septum, behind shoulder blotch (Fig. 9B), followed by banding along dorsum and 2–3 indistinct blotches below horizontal septum (Fig. 9C), interspaces silver to pale blue; head with few markings, melanophores scattered over brain, dark band forming between orbit and maxilla; fins mostly hyaline, sparse melanophores and underlying xanthophores visible along spines.

Colour notes. A distinctive species with few ontogenetic changes in juvenile colouration, capable of rapid pattern changes within 1–3 seconds. At 20–30 mm: snout and dorsum intense yellow-tan, head and body abruptly silvery off-white ventrally, lateral-line cryptic; 4 narrow primary stripes along flank, of similar widths, terminating near base of caudal peduncle, golden orange in captivity or when freshly killed (Pl. 1E), orange (rarely orange-tan) in field with dorsal stripe concealed by 3–4 pale brown to grey blotches (Pl. 1F,G), interspaces silver (rarely pale blue, Pl. 1F); intense banding frequently displayed in field with concomitant partial-fading of primary stripes (Fig. 3A), dulled in captivity and after death (cf. Pl. 1E and 1G), 4–6 narrow bands along dorsum, series of blotches along ventral margin of lateral-line, further banding between blotches and belly (Pl. 1G); blotch below dorsal spines forming diagnostic shoulder blotch (Fig. 5A), cuboidal with pointed tip extending over lateral-line and surrounded by silvery halo (Pl. 1F); intense dark mid-lateral stripe prevalent in field, width approximately 5.0 in body depth, rarely accompanied by banding or primary stripes; snout and cheek without dark markings, intermittent near-vertical black band bisecting eye in field; fins mostly hyaline, dorsal fin often similar hue to dorsum in field, sparse off-white and dark patches over anterior half of spinous fins. At 20–30 mm, individuals in field frequently display background and primary-stripe colourations either with distinct shoulder blotch alone or without dark markings (as in Pl. 6, p. 173 in Masuda & Kobayashi [1994]).

At 30–80 mm: mostly as in smaller individuals, dorsum greyish tan, banding more intense than when smaller, shoulder blotch and orange primary stripes prominent; two vertical dark tan bands visible on suborbital at greater than 35 mm (Fig. 3A, Pl. 1G), third similar band along rear margin of preoperculum.

Colour in alcohol. At 16–21 mm, late pre-settlement: body translucent off-white to pale straw, xanthophore

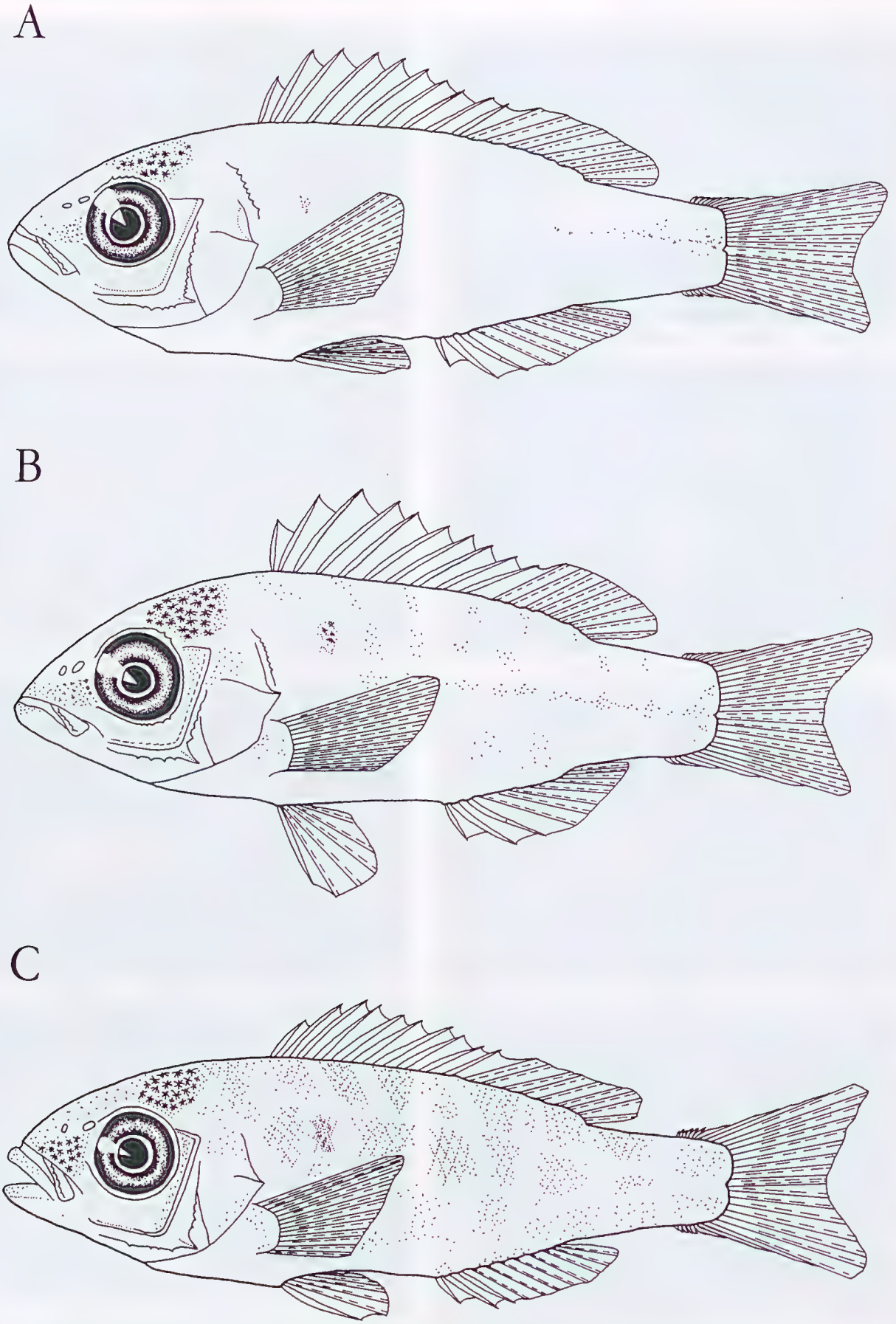

Fig. 9. Ontogenetic changes in the external melanophore pigmentation of *Lethrinus genivittatus* prior to settlement. Typical length ranges: A—16–20 mm SL; B—17–20 mm SL; C—18–21 mm SL. Details of scalation, myomeres and internal pigmentation not shown. Based on six specimens from Green Island, including AMS I.34915-001, AMS I.34916-001, AMS I.34917-002 and 2 specimens not retained.

pigmentation lost, melanophores retained in similar patterns to when freshly killed, fins hyaline. At greater than 20 mm, post-settlement: body and head pale grey-tan, belly off-white; dorsal banding slightly dulled, dark blotches below lateral-line indistinct; shoulder blotch faded from when freshly killed, halo absent; primary stripes lost; fins hyaline.

Ecology. At less than 90 mm, common in dense shallow seagrass beds on coral reefs and in coastal embayments (0.2–3.0 m; *Cymodocea, Halodule, Halophila, Thalassia, Zostera*); settlers recorded from 16 mm although typically 19–22 mm, mostly solitary, individuals 20–30 mm hover over the seagrass canopy, periodically picking food items off seagrass blades, occasional aggression noted towards conspecifics and congeners of a similar size; not appearing site-attached although seldom moving further than 1 m when disturbed, at less than 30 mm will rapidly seek shelter at base of canopy if closely approached; at greater than 30 mm occasionally joining loose multi-species schools with *Scarus* species (Scaridae), *Parupeneus indicus, Siganus fuscescens* and congeners of a similar size.

Field identification. Although distinctive when freshly killed, may be easily confused with *L. obsoletus* under field conditions, particularly at less than 40 mm. Both species are capable of rapid changes in their overlying dark colour patterns and display 3–4 coloured primary stripes. When recently-settled (18–25 mm), *L. genivittatus* and *L. obsoletus* often display an almost uniform yellow-tan to grey-tan hue, and observation for several minutes is necessary before other patterns can be discerned. The shoulder blotch's form is useful for distinguishing these species (Fig. 5.): the *L. obsoletus* shoulder blotch is mostly vertically-rectangular, does not cross the lateral-line and is seldom surrounded by a pale halo. This contrasts with the square shoulder blotch with pointed extension over the lateral-line and pale halo in *L. genivittatus*. At less than 40 mm, dorsal bands tend to be narrower and of sharper definition in *L. genivittatus* than *L. obsoletus* (cf. Pl. 1G and 2E). In many cases, it may be necessary to collect smaller specimens for confirmation with morphological characters or freshly-killed colour patterns.

Identification notes. Carpenter & Allen (1989) report the degree of outward-curvature of the lower canine teeth, along with the greater length of the second dorsal spine over the third, to be the most useful means for separating *L. genivittatus* from other lethrinids. However, dentition is of little value for distinguishing *L. genivittatus* at less than 80 mm. Although the second dorsal spine is shorter than the third until 30–35 mm in most cases ("Diagnosis" above), it is still relatively elongate in individuals greater than 23 mm in comparison with other *Lethrinus* species, and may be a useful diagnostic character. The number of scale rows above the lateral-line also differentiates *L. genivittatus* (4.5) from similar species such as *L. obsoletus* (5.5).

Previous descriptions. Early life history stages of *L. genivittatus* have been described and/or figured in several works. The larval development of laboratory-reared individuals 2.7–16.4 mm was described and figured (as *L. nematacanthus*) by Mori (1988), although few details of pigmentation were given. Juvenile colour plates were provided by Kuiter (1993, length not given), Masuda & Kobayashi (1994, 35 mm total length) and Kuiter & Debelius (1994, 40 mm, reproduced here in Pl. 1G). Sato (1984) noted the prolonged occurrence of maxillary serrations in *L. genivittatus* juveniles (under *L. nematacanthus*) as "maxillary ornamented with row of tubercles in younger individuals".

Lethrinus harak (Forsskål)

Pl. 1H, 2A,B

Material examined. (38 specimens: 19–96 mm). AUSTRALIA Cocos-Keeling Islands, AMS I.33529-002 (1:73 mm); Great Barrier Reef region, AMS I.20773-026 (2:93–96 mm), AMS I.34911-005 (5:24–56 mm), AMS I.34912-004 (1:19 mm), AMS I.34912-005 (1:21 mm), AMS I.34920-001 (1:20 mm), AMS I.34920-002 (1:20 mm), USNM 336682 (3:23–34 mm), USNM 336683 (2:19–21 mm), not retained (9:25–67 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-048 (6:45–84 mm), AMS I.17075-003 (1:43 mm); SOLOMON ISLANDS Guadalcanal, AMS I.17482-020 (5:62–76 mm).

Diagnosis. Body moderately deep, depth 2.7–3.1 in SL; 5.5 dorsal scale rows, 14–15 ventral scale rows; maxillary serrations 1–3 at 22–25 mm, absent at greater than 35 mm; cheek scales retained until 45 mm; dorsal spine 5 (occasionally 4) the longest.

Diagnostic colour notes. Dorsum olive to off-white-tan, silvery blue interspaces prominent at 18–22 mm (Pl. 1H); dark horizontal blotch below dorsal spines 8–10, inconspicuous at 18–22 mm, seldom switched off; shoulder blotch square, usually inconspicuous; dark mid-lateral stripe moderately-intense, seldom obscuring horizontal blotch, width approximately 4.0 in body depth; fins mostly hyaline.

Colour notes. A relatively distinctive species, capable of rapid colour changes within 1–3 seconds. At 18–22 mm (Pl. 1G): dorsum and nape yellowish olive, series of diffuse black markings (3 bands followed by 3 blotches) above lateral-line, 2–3 exceedingly-faint black bands along caudal peduncle, 3–4 yellowish olive blotches along lower lateral-line margin, interspaces silvery blue, rectangular blotch below dorsal spines 8–10 beginning to form characteristic *L. harak* "thumb-print" blotch, series of indistinct blotches of similar hue between pectoral and anal fins, belly silvery off-white; snout and lips dusky olive, cheek silvery off-white, without dark markings, eye often bisected by near-vertical black band

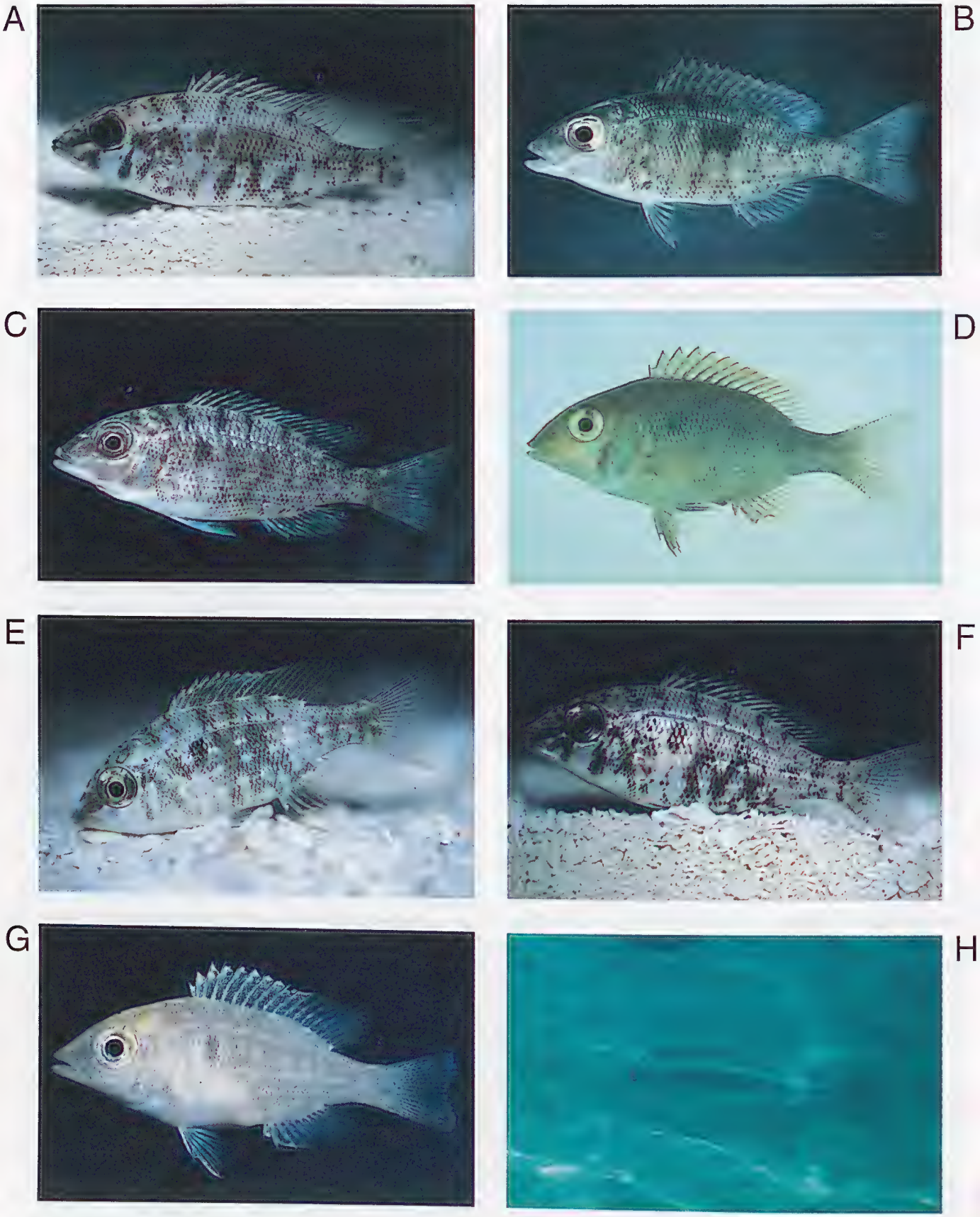

Plate 2. **A**—*Lethrinus harak*, 55 mm SL, live (stress colouration), Green Island. **B**—*Lethrinus harak*, 50 mm SL, dead, Green Island. **C**—*Lethrinus lentjan*, 50 mm SL, live, Green Island. **D**—*Lethrinus nebulosus*, 30 mm SL, dead, Ken-Ting National Park (Taiwan), reproduced from Shao *et al.* (1992). **E**—*Lethrinus obsoletus*, 25 mm SL, AMS I.34913-004, live, Green Island. **F**—*Lethrinus obsoletus*, 56 mm SL, live, Green Island. **G**—*Lethrinus obsoletus*, 27 mm SL, AMS I.34913-005, dead, Green Island. **H**—*Lethrinus obsoletus*, approx. 250 mm SL, underwater photograph, Green Island.

in field; fins mostly hyaline, off-white with diffuse dark blotches over anterior half of spinous fins. After death, patterns retained though faded.

At 23–80 mm (Pl. 2A,B): body and head olive to grey-tan dorsally, belly off-white; dark banding and blotches more distinct, intensifying when stressed (Pl. 2A), most fading after death (Pl. 2B), rapidly switched on or off, "thumb-print" blotch distinct, cuboidal shoulder blotch below dorsal spines 4–5, rarely conspicuous, dark blotches between pectoral and anal fins now as series of 3–4 short bands, terminating mid-body; dark mid-lateral stripe often displayed in field, dark khaki, seldom fully obscuring "thumb-print" blotch, width approximately 4.0 in body depth; cheek silver to off-white, series of dark bands when stressed (Pl. 2A), intermittent dark band through eye until 60 mm; fins hyaline greyish yellow, margins often pink to pale scarlet in field. At greater than 80 mm, dark mid-lateral stripe absent, banding faded or absent, "thumb-print" blotch distinct.

Colour in alcohol. Body and head pale off-white-tan, belly off-white; dark body and head markings dulled, "thumb-print" blotch often inconspicuous at less than 23 mm; fins hyaline, melanophore patterns retained.

Ecology. Common, restricted to reef seagrass cover at less than 80 mm, without preference for particular seagrass species or canopy structures, larger juveniles also found over adjacent sand/coral rubble and sparse vegetative growth (*Halimeda, Sargassum*); settlers 16–18 mm, mostly solitary, not appearing site attached, rapidly seek cover within the seagrass canopy when disturbed; at greater than 40 mm, occasionally found with similarly-sized juveniles of *Parupeneus barberinus* and *P. indicus, Siganus fuscescens* and congeners (particularly *L. atkinsoni, L. obsoletus, L. genivittatus*) in small loose schools, no aggressive interactions noted; observed resting on the substrate among seagrass shoots after dark, not fleeing when approached.

Field identification. Generally an easily identified species, distinguished at greater than 25 mm by presence of the dark "thumb-print" blotch and the absence of coloured primary stripes. If intense banding is displayed, then the horizontal blotch is always visible. At less than 25 mm (Pl. 1H), the series of khaki blotches below the lateral-line, pale blue interspaces, and lack of primary stripes and intense mid-lateral stripe is diagnostic of *L. harak*. Small individuals often need to be followed for several minutes to confirm their identification.

Previous descriptions. The early juvenile stage of *L. harak* has not been described previously. Masuda & Kobayashi (1994) included a colour plate of a specimen 40 mm total length.

Lethrinus lentjan (Lacépède)

Pl. 2C, Fig. 5B,C

Material examined. (8 specimens: 24–105 mm). AUSTRALIA Great Barrier Reef region, AMS I.22700-041 (1:78 mm), AMS I.34144-001 (2:75–105 mm), AMS I.34911-006 (1:24 mm), AMS I.34911-007 (1:39 mm), AMS I.34912-006 (1:27 mm), AMS I.34920-003 (1:46 mm), AMS I.34921-001 (1:31 mm).

Diagnosis. Body moderately deep, depth 2.5–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 3–5 at 24 mm, 1–2 at 31 mm, absent by 39 mm; cheek scales absent at greater than 26 mm; dorsal spine 4 (rarely 5) the longest at 24–105 mm.

Diagnostic colour notes. Body and head silvery olive to greyish tan, belly off-white; dark markings moderately-intense, often inconspicuous, shoulder blotch small, cuboidal or circular, width of dark mid-lateral stripe approximately 5.0 in body depth; 3–4 narrow primary stripes of similar widths, pale pink to orange-pink, often inconspicuous (as in Pl. 2C), interspaces silver; rear margin of operculum with narrow scarlet patch at greater than 40 mm (Pl. 2C); fins mostly hyaline.

Colour notes. A relatively drab species, possessing only subtle differences in juvenile colouration from several other species ("Field Identification" below), capable of rapid pattern changes within 2–3 seconds. At 25–31 mm: dorsum pale olive, belly off-white, lateral-line cryptic, 3–4 narrow primary stripes along flank, of similar width and intensity, pale pink to orange-pink with silver interspaces, often inconspicuous (as in Pl. 2C), intermittent dark patterns on body less intense than similar species (e.g., *L. obsoletus*), 5–6 indistinct dark bands along dorsum between head and caudal peduncle, most extending to lateral-line, 2–3 similar bands along caudal peduncle, dorsal bands may connect with diffuse banding and series of 3–4 blotches along mid-body, first blotch below dorsal spines 3–4 forming diffuse cuboidal or circular shoulder blotch (Fig. 5B), never with pale halo; head similar to body, operculum and cheek silvery off-white, near-vertical black band often bisecting eye in field, may join diffuse grey blotch below eye, rear margin of preoperculum occasionally with narrow dark band (or as several dark blotches); fins mostly hyaline, few dark markings, outer margins pale pink in field, scattered off-white and dark patches in captivity (as in Pl. 2C) or after death.

At 40–60 mm (Pl. 2C): body pale grey-tan, lateral-line cryptic or lined either side by row of silver dots, dark banding and blotches along body more distinct; dark mid-lateral stripe occasionally displayed in field, dark grey, width approximately 5.0 in body depth; snout pale tan, occasionally several silvery bands across snout, narrow scarlet patch along the rear margin of operculum, distinguishable in field though often faded in captivity (Pl. 2C) or after death; primary stripes more distinct (faded in Pl. 2C); fins mostly hyaline, often deep pink hue along fin

margins in field, darkening to pale purple after death, diffuse patches of melanophores along dorsal and anal spines.

At 60–100 mm: dorsum olive, belly off-white, few or no dark markings, banding and shoulder blotch faint or absent when alive, diffuse after death, dark mid-lateral stripe absent, primary stripes faded or absent, scarlet operculum margin bright.

Colour in alcohol. At 24–60 mm, body and head creamy tan, scattered with fine black flecks, slightly paler ventrally; shoulder blotch retained, other dark markings on body faint or lost, lateral-line cryptic; primary stripes lost, at 40–80 mm may be replaced by stripes slightly darker or paler than adjacent body in specimens preserved for less than 1 year; fins hyaline, dark markings retained though faint. Preserved specimens (20–80 mm) may be indistinguishable from *L. obsoletus* and *L. nebulosus*, precluding diagnoses beyond *L. lentjan/obsoletus/nebulosus*.

Ecology. Uncommon at Green Island, settles into shallow seagrass cover, remaining there until 80–100 mm, at 100–140 mm only recorded within shoreline seagrass habitats after dark; not appearing site attached, mostly solitary although occasionally joining small (approximately 10–15 individuals) multi-species schools with congeners (principally *L. atkinsoni, L. harak* and *L. obsoletus*), siganids and mullids of a similar size; other field behaviours unknown.

Field identification. A difficult species to identify in the field, displaying similar colouration to both *L. obsoletus* and *L. nebulosus*. All three species possess a similar body profile and may join multi-species schools together. The colouration differences for distinguishing these species in the field are summarised below:

Lethrinus lentjan (Pl. 2C, Fig. 5B,C): dark body markings moderately-intense, shoulder blotch circular or square, rarely vertically-rectangular; 3–4 primary stripes, narrow, of similar widths, pink to orange-pink, often indistinguishable at less than 35 mm, interspaces silver; rear margin of operculum scarlet at greater than 40 mm; spinous fin membranes mostly hyaline.

Lethrinus nebulosus (Pl. 2D, Fig. 5C,D): dark body markings moderately-intense, shoulder blotch circular or square; more than 4 narrow primary stripes, pale blue, mostly indistinguishable at less than 40 mm, interspaces off-white to yellow-tan; operculum off-white silver or yellow-tan; spinous fin membranes with moderately-dense melanophores.

Lethrinus obsoletus (Pl. 2E–G, Fig. 5B,C,E): dark body markings usually intense; shoulder blotch square or vertically-rectangular; primary stripes 3–4, orange-tan, pectoral stripe wider than others, visible at greater than 20 mm, interspaces off-white; operculum silvery off-white; spinous fin membranes mostly hyaline.

These combinations of field colours will allow most *L. lentjan* juveniles to be separated from *L. obsoletus* at greater than 20 mm, and from *L. nebulosus* at greater than 40 mm. Nonetheless, at less than 40 mm, the collection of specimens for examination of colours displayed when freshly killed, or to allow them to be grown to a larger size in aquaria, is recommended.

Lethrinus lentjan is one of the few lethrinids to occur as recently-settled or older juvenile stages in coastal seagrass habitats throughout northern Australia (Blaber *et al.*, 1992). In such localities its identification is facilitated by the absence of *L. obsoletus*, although it should be noted that *L. nebulosus* juveniles are also known from similar areas (Blaber, 1980).

Identification note. The presence of cheek scales may distinguish *L. lentjan* and *L. obsoletus* as early juveniles. Cheek scales were only noted on a single *L. lentjan* specimen of 24 mm (absent at 26–46 mm, cf. present until 30–39 mm in *L. obsoletus*).

Lethrinus nebulosus (Forsskål)

Pl. 2D, Fig. 5C,D

Material examined. (4 specimens: 38–62 mm). AUSTRALIA Great Barrier Reef region, AMS I.34924-001 (1:62 mm), AMS I.34925-001 (1:38 mm). Provisional identification: Great Barrier Reef region, AMS I.431 (2: 47–48 mm).

Diagnosis. At 38–62 mm, body moderately deep, depth 2.6–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations absent; cheek scales absent; dorsal spine 4 or 5 the longest.

Diagnostic colour notes. Dorsum grey-tan at 30–38 mm, yellow-tan at 62 mm; lateral-line cryptic or with dorsal row of silvery dots; shoulder blotch vertically-rectangular or square; more than 4 narrow primary stripes, pale blue, indistinct at 30–38 mm; 2 pale blue stripes between mouth and orbit; spinous fins greyish yellow anteriorly, dark grey when folded at rest.

Colour notes. A distinctive species throughout most of the juvenile period, although difficult or impossible to distinguish when recently-settled, capable of rapid colour pattern changes, details of dark mid-lateral stripe pattern unknown. At 30–62 mm (Pl. 2D): dorsum grey-tan to yellow-tan, shading ventrally to off-white belly, lateral-line cryptic, bordered dorsally by row of diffuse silvery dots; dark banding moderately intense in field, may fade after death (Pl. 2D), rapidly switched on or off within 1–3 seconds, 3–5 indistinct dorsal bands between head and caudal peduncle, most connecting with diffuse banding below lateral-line, 2–3 bands along caudal peduncle; shoulder blotch below dorsal spines 4–5, square or vertically-rectangular (Fig. 5C,D), indistinct when alive, not bordering lateral-line; from 38 mm, primary stripes forming along flank as more than 4 rows of faint pale blue dots, between operculum or pectoral-base and caudal peduncle, may appear as faint stripes when freshly collected or killed; head similar to body, rear margin of

preoperculum dark grey after death (Pl. 2D), cheek pale yellow-tan, near-vertical intermittent black band through orbit in field, faded at death, 2 silvery blue stripes between mouth and lower orbit margin; fins mostly hyaline, spinous fins greyish yellow anteriorly, dark grey when folded at rest.

Colour in alcohol. Body pale off-white tan, belly off-white; dark head and body markings retained, shoulder blotch distinct, primary stripes faint, dorsal row of pale dots along lateral-line grey; dense melanophores retained on fins, other hues lost. After preservation, *L. nebulosus* juveniles of less than 80 mm are often indistinguishable from *L. lentjan* and *L. obsoletus*. Identification of such material should at most be considered provisional (see also *L. obsoletus* "Identification note"). The moderate to dark grey hue of spinous fin membranes may separate preserved *L. nebulosus* from *L. obsoletus/lentjan*.

Ecology. Juveniles uncommon at Green Island, occasionally observed over the shoreline seagrass habitat at 40–120 mm, never over non-seagrass habitats; mostly solitary, occasionally joining small schools of similarly-sized congeners, particularly *L. obsoletus* and *L. harak*, no aggressive interactions noted, other field behaviours unknown; a 62 mm specimen was collected over sand adjacent to fringing reef, 3 m, Lizard Island lagoon; also known from inshore habitats (Blaber, 1980).

Field identification. At 30–38 mm, difficult to distinguish in the field, the characteristic primary and preorbital stripes may be faintly visible when freshly collected (as in Pl. 2D). At 62 mm, the pale blue preorbital stripes, yellow-tan body, and to a lesser extent the primary stripes, are clearly visible and diagnostic. However, individuals 30–100 mm readily display dark intermittent banding which may obscure any underlying colouration. In most cases, specimens will need to be observed for at least several minutes before their identification can be accurately discerned.

At less than 40 mm, distinguishing *L. nebulosus* juveniles from *L. lentjan*, and occasionally *L. obsoletus*, is difficult or impossible prior to development of distinct primary stripes. It is often necessary to collect such individuals for maintenance in aquaria to allow examination of colour patterns displayed with subsequent growth. The combinations of colour patterns most useful for separating *L. nebulosus* juveniles from these congeners are summarised in the "Field Identification" section of *L. lentjan*.

Previous descriptions. Wheeler (1961) sketched and briefly described the colour patterns displayed by two "small" captive individuals, and Carpenter & Allen (1989) included a brief juvenile colour description and accompanying colour plate (length of specimen not given). Allen & Swainston (1988) and Kuiter (1993) also provided juvenile colour plates. Shao *et al.* (1992) included a colour plate of a 30 mm juvenile (reproduced here in Pl. 2D), illustrating the early appearance of the characteristic primary stripes. Two further juveniles from Taiwan (83 and 105 mm) are shown in Lee (1993).

Lethrinus obsoletus (Forsskål)

Pl. 2E–H, Fig. 5B,C,E

Material examined. (72 specimens: 17–81 mm). AUSTRALIA Great Barrier Reef region, AMS I.20772-027 (1:81 mm), AMS I.34911-008 (4:18–27 mm), AMS I.34911-009 (3:36–39 mm), AMS I.34911-010 (1:33 mm), AMS I.34912-009 (1:33 mm), AMS I.34913-003 (1:25 mm), AMS I.34913-004 (1:25 mm), AMS I.34913-005 (1:27 mm), AMS I.34913-006 (1:43 mm), AMS I.34919-002 (2:31–35 mm), AMS I.34919-003 (1:31 mm), AMS I.34926-001 (1:18 mm), AMS I.34927-001 (1:58 mm), USNM 336685 (1:20 mm), USNM 336686 (3:26–34 mm), USNM 336687 (4:37–40 mm), not retained (45:17–63 mm).

Diagnosis. Body moderately deep, depth 2.5–3.0 in SL; 5.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 5–7 at 16–18 mm, 1–4 at 25–29 mm, 0–2 at 30–39, absent thereafter; cheek scales present at 16–30 mm, variable at 31–39 mm, absent at less than 39 mm; dorsal spine 4 or 5 the longest at less than 35 mm.

Diagnostic colour notes. Body and head cream to pale grey-tan; banding intense, shoulder blotch cuboidal or vertically-rectangular, seldom with pale halo, not crossing lateral-line; dorsal margin of lateral-line silvery cream; 2–4 orange-tan primary stripes, pectoral stripe of greatest width and intensity; dark mid-lateral stripe frequently displayed (20–80 mm), intense, width approximately 5.0 in body depth; fins mostly hyaline.

Colour notes. Minimal change in colour patterns throughout juvenile ontogeny, frequently displays dark intermittent patterns, able to switch colour patterns in 1–3 seconds. At 17–19 mm, recently-settled: body cream, abdomen silver, lateral-line cryptic; 4–7 indistinct grey bands along dorsum, may join faint ventral bands at lateral-line; shoulder-blotch dark grey, often inconspicuous, cuboidal (Fig. 5B), never crossing lateral-line, without pale halo, rapidly switched on or off within 2–3 seconds; 2–3 indistinct primary stripes, pale orange-tan, dorsal and ventral stripes often indistinguishable, pectoral stripe marginally wider than orbital stripe; nape and snout yellow-tan, cheek silver without dark markings; fins hyaline.

At 20–80 mm (Pl. 2E–G): body pale grey-tan, belly off-white, lateral-line usually distinct, dorsal margin off-white; banding and shoulder blotch distinct and intense when alive (Pl. 2E,F), fading after death (Pl. 2G), medial dorsal bands usually joining 2–3 cuboidal blotches below lateral-line (Pl. 2E,F), ventral bands extending diagonally between blotches and belly, shoulder blotch distinct, mostly vertically-rectangular (Fig. 5C,E, Pl. 2F,G), occasionally cuboidal (Fig. 5B, Pl. 2E), seldom bordering lateral-line, rarely with pale halo; dark mid-lateral stripe frequently seen in field, dark brown to black, width approximately 5.0 in body depth; primary stripes orange-pink to orange-tan, dorsal stripe seldom conspicuous, pectoral stripe

slightly wider than others (as in Pl. 2G); head similar to body, nape and snout uniform or mottled tan, black near-vertical band often bisecting orbit in field, grey blotch below orbit from 22 mm (inverted v-shaped band from 45 mm) and dark grey to brown blotches along rear margin of preoperculum and operculum in captivity; fins mostly hyaline, pale pink distally in field, anterior half of spinous fins off-white with scattered brown patches.

Colour in alcohol. At 17–20 mm, body off-white, dark banding and shoulder blotch dulled, primary stripes lost, fins hyaline; at greater than 25 mm, body and head olive to grey-tan, belly off-white, banding and dark head markings distinct though dulled, primary stripes lost; fins hyaline. After preservation, *L. obsoletus* juveniles (18–80 mm) are often indistinguishable from *L. lentjan* and *L. nebulosus*, preventing identification beyond *L. obsoletus/ lentjan/nebulosus*.

Ecology. Common, mostly solitary, occasionally joins small (approximately 10–15 individuals) multi-species schools with similarly-sized congeners (*L. atkinsoni, L. genivittatus, L. harak, L. variegatus*), *Stethojulis strigiventor, Parupeneus barberinus* and *P. indicus*, and particularly *Siganus fuscescens*; settles at 16–18 mm into shallow seagrass cover (0.2–4 m; *Halodule, Thalassia, Cymodocea*) on fringing and lagoonal reefs, an ontogenetic shift apparent to adjacent reef-flat habitats at 70–90 mm, individuals 90–140 mm only occasionally encountered within shallow areas; forages diurnally off seagrass leaves (18–30 mm) or on benthic items (at greater than 30 mm), no aggressive interactions noted, individuals 18–25 mm rapidly seek shelter within the seagrass canopy when disturbed.

Field identification. Generally an easy species to identify in the field, although can be confused with *L. genivittatus, L. lentjan* and *L. nebulosus* (Table 1). Small specimens (18–25 mm) can be distinguished from *L. nebulosus* and *L. lentjan* by their intense shoulder blotch (Fig. 5) and orange to orange-tan primary stripes. At this size, *L. obsoletus* and *L. genivittatus* can be reliably separated by their primary stripes, dorsal bands, and shoulder blotch. At greater than 25 mm, *L. obsoletus* can be distinguished from other species by the prominent orange-pink to orange-tan pectoral stripe. During display of the dark mid-lateral stripe, the off-white dorsal border of the lateral-line, in combination with a moderately-deep body profile (cf. pale dorsal border with slender body in *L. variegatus*), is diagnostic. At all sizes, individuals may need to be observed for several minutes before the full range of colour patterns can be ascertained. At less than 40 mm, the collection of specimens for examination of freshly-killed colours may also be necessary. Further notes on separating these species in the field are given in the "Field Identification" sections of *L. genivittatus* and *L. lentjan*. *Lethrinus obsoletus* appears unique among GBR lethrinids in continuing to display a dark mid-lateral stripe pattern throughout the adult stage (Pl. 2H).

Previous descriptions. Wheeler (1961) included a colour sketch of a captive 88 mm TL specimen (as *Lethrinus ramak*) along with brief descriptions of the stress, resting and freshly-killed colouration displayed by "very young" specimens (sizes not given). Masuda & Kobayashi (1994) provided a colour plate of a specimen 35 mm total length.

Identification notes. Carpenter & Allen (1989) note the presence of a "knob" on the outer surface of the maxilla in *L. obsoletus* to be useful for separating this species from other lethrinids. This character is indistinguishable at less than 80 mm. Alternative meristic and morphological measurements (particularly the number of dorsal scale rows, presence of cheek scales and number of maxillary serrations), along with the shoulder blotch and primary stripes, represent the easiest means of distinguishing smaller *L. obsoletus* from other close species.

Lethrinus olivaceus Valenciennes

Pl. 3A,B, Fig. 3C,D

Material examined. (15 specimens: 32–124 mm). AUSTRALIA Great Barrier Reef region, AMS I.34919-004 (1:36 mm), AMS I.34928-001 (1:38 mm), AMS I.34929-001 (1:39 mm), AMS I.34930-001 (1:32 mm), AMS I.34931-001 (1:40 mm), AMS I.34931-002 (1:63 mm), USNM 336688 (1:34 mm), USNM 336689 (1:53 mm), USNM 336690 (1:32 mm), not retained (5:44–124 mm); INDONESIA Eastern Archipelago, NMV 46333 (1:111 mm).

Diagnosis. Body moderately elongate, body depth 2.9–3.2 in SL; 5.5 dorsal scale rows, 16–17 ventral scale rows; maxillary serrations absent at greater than 32 mm; cheek scales retained until 40 mm; dorsal spine 3 or 4 the longest.

Diagnostic colour notes. Dorsum pale olive-grey, shading to silvery off-white ventrally; dark markings intense, shoulder blotch horizontally-rectangular, ventral bands diagonal (Fig. 3D, Pl. 3B), width of dark mid-lateral stripe approximately 6.0 in body depth; single dark blotch below orbit at 40–63 mm, 2 blotches below orbit and 2 bands between mouth and orbit at 124 mm; spinous fins with dense melanophores, appearing dark grey when folded at rest.

Colour notes. At 32–63 mm: dorsum off-white tan to olivaceus tan, body silvery off-white ventrally, lateral-line mostly cryptic, occasionally faded yellow-tan stripe along ventral margin; dark markings prominent, particularly in field (as in Pl. 3B), rapidly switched on in 1–3 seconds when approached or otherwise disturbed, 5–7 indistinct dark bands along dorsum between head and caudal peduncle, 2–3 similar bands along caudal peduncle, 2–3 dark blotches below lateral-line, first blotch of greatest intensity forming a horizontally-rectangular shoulder blotch below dorsal spines 5–7 (Fig. 3D, visible though faded in Pl. 3A,B), network of diagonal dark bands between blotches and belly (Fig. 3D); intense dark mid-lateral stripe

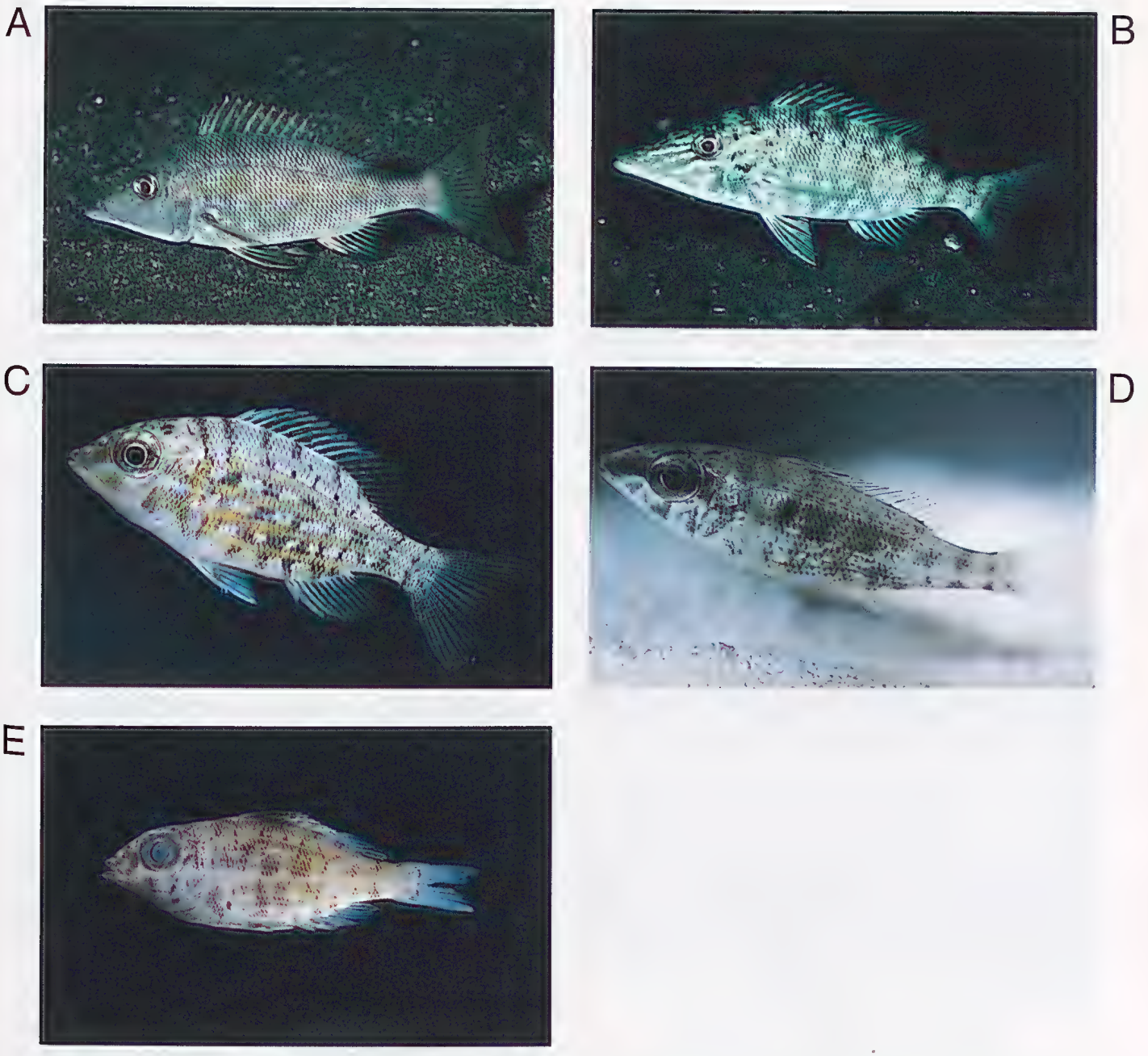

Plate 3. **A**—*Lethrinus olivaceus*, approx. 250 mm SL, underwater photograph by R.H. Kuiter, Bali (Indonesia). **B**—*Lethrinus olivaceus*, approx. 400 mm SL, underwater photograph by R.H. Kuiter, Papua New Guinea. **C**—*Lethrinus ornatus*, 36 mm SL, AMS I.34932-001, live, Green Island. **D**—*Lethrinus variegatus*, 39 mm SL, live, Green Island. **E**—*Lethrinus xanthochilus*, 26 mm SL, AMS I.34923-001, dead, Green Island.

common in field, banding switched off, narrower than that of other lethrinids, width 6.0 in body depth, switched on or off rapidly; lips, snout and nape mottled grey, preoperculum and ventral half of operculum silvery white with indistinct dark blotches along posterior margins, further dark blotch forming below orbit; fins mostly hyaline, anterior half of spinous fins with off-white and yellow patches interspersed by dark grey blotches, pale orange-pink distally at greater than 40 mm, appearing dark grey when folded at rest.

At 124 mm, as in smaller specimens, dark markings on head and body more intense, 5–6 dark blotches on operculum, 2 dark blotches below orbit and 2 bands between mouth and orbit; fins with oblique maroon bands, interspaces off-white yellow, pale scarlet distally.

Colour in alcohol. Dorsum pale off-white tan, shading to off-white belly; distinctive markings on body and head slightly faded; dense melanophores retained on fins.

Ecology. Uncommon at Green Island, restricted to shoreline seagrass areas (0.2–1.5 m; *Cymodocea, Halodule, Thalassia*), occurring over shallow (2–4 m)

open sand/coral rubble at greater than 100 mm; not appearing site-attached, a single 35 mm individual was observed swimming in a loose multi-species school with similar-sized *Siganus fuscescens, Halichoeres* species (Labridae) and congeners (*L. atkinsoni, L. harak, L. obsoletus)*, periodically picking food items off seagrass blades and adjacent substratum; no aggressive interactions noted, other field behaviours unknown.

Field identification. Rarely encountered in the field as early juveniles, a combination of the slender body and snout profiles, horizontal shoulder blotch, narrow mid-lateral stripe, ventral diagonal banding and absence of coloured primary stripes may distinguish this species. The intense fin pigmentation characteristic of dead specimens was not noted in field observations, although is faintly visible in the colour plate of a 150 mm juvenile given in Myers (1989). During display of the dark mid-lateral stripe pattern, *L. olivaceus* may be confused with numerous species, particularly *L. genivittatus*. Individuals may need to be followed for several minutes before other patterns are displayed.

Previous descriptions. Kuiter & Debelius (1994) included a colour plate of *L. olivaceus* (as *L. microdon*) showing the characteristic horizontal shoulder blotch and ventral banding. A 150 mm juvenile (as *L. semicinctus*) is shown in Myers (1989, Pl. 56E), displaying the intense shoulder blotch and narrow mid-lateral stripe characteristic of field observations. Lieske & Myers (1994, Pl. 53) also figured the *L. olivaceus* dark mid-lateral stripe pattern.

Remarks. Freshly collected *L. olivaceus* juveniles are unlikely to be confused with other *Lethrinus* species of a similar size. Specimens retained frozen or in alcohol for extended periods were noted to display near-identical banding to *L. genivittatus*, particularly if the orange primary stripes in the latter species had faded. Such material may be reliably separated using the number of dorsal scale rows, shape of the shoulder blotch, and intensity of pelvic-fin pigmentation.

Lethrinus ornatus Valenciennes

Pl. 3C

Material examined. (11 specimens: 20–91 mm). AUSTRALIA Great Barrier Reef region, AMS I.34917-001 (1:32 mm), AMS I.34932-001 (1:36 mm), not retained (6:20–69); INDONESIA Maumere Bay (Flores), not retained (2:20 mm); SOLOMON ISLANDS New Georgia Island, AMS I.22128-154 (1:91 mm).

Diagnosis. Body relatively deep, its depth 2.5–2.8 in SL; 5.5 dorsal scale rows, 15 ventral scale rows; maxillary serrations 2–4 at 20 mm, absent at greater than 28 mm; dorsal spine 5 the longest at 20–60 mm (rarely 4 at greater than 50 mm).

Diagnostic colour notes. Primary stripes 4, bright orange, of similar width and intensity, interspaces silvery off-white; fins hyaline, pink to pale scarlet distally; pale scarlet band along rear margin of operculum at greater than 28 mm; dark markings seldom displayed.

Colour notes. A striking species with few differences in colouration between adults and juveniles, difficult to confuse with other *Lethrinus* species. At 20–80 mm (Pl. 3A): dorsum and nape pale grey-tan, flank silvery off-white, belly off-white; 4 prominent bright orange primary stripes, of similar width and intensity, fine grey borders, interspaces grey-tan or silvery off-white, dorsal stripe extending to below medial dorsal rays, remaining stripes terminating at base of caudal peduncle; black banding and cuboidal shoulder blotch seldom displayed in field although common at capture (Pl. 3C) and after death, rapidly switched on or off, 6–7 bands along dorsum, most connecting with further banding between lateral-line and belly, 2–3 similar bands along caudal peduncle; dark mid-lateral stripe occasionally displayed in field, dark grey, width approximately 4.0 in body depth, obscuring dorsal and orbital stripes, pectoral and ventral stripes usually remaining visible though dulled; head similar to body, snout yellow-brown, cheek silvery off-white, may have diffuse tan blotch, eye often bisected by near-vertical black band in field, pale scarlet band developing along rear margin of operculum from 28 mm (faded in Pl. 3C); fins mostly hyaline, caudal and pectoral fins pale pinkish yellow, anterior half of spinous fins off-white with dark grey patches basally, deep pink to scarlet distally in field, diffuse pink at capture (as in Pl. 3C) and when freshly-killed.

At greater than 80 mm, body, head and fins as in smaller specimens, dark mid-lateral stripe and banding absent.

Colour in alcohol. Dorsum pale grey-tan with 5–6 dark bands; ventral half of body and primary stripes faded to off-white, dark banding below lateral-line dissected by primary stripes into 3–6 series of square blotches; banding retained along caudal peduncle; fins hyaline.

Ecology. Uncommon at Green Island, settles at 19–21 mm into shallow reef seagrass habitats, remaining there until 70–80 mm; solitary, not appearing site attached, seldom in close association with other fishes, occasionally joining small loose schools with juvenile *Stethojulis strigiventor, Siganus fuscescens, Parupeneus indicus* and congeners of a similar size, particularly in the presence of piscivorous carangids or lutjanids; at 40–70 mm periodically resting briefly at the base of the seagrass canopy in tall-dense *Cymodocea* and *Halodule*, fleeing over the canopy when disturbed.

Field identification. Juvenile *L. ornatus* are best distinguished in the field by their deep body profile, intense orange primary stripes and rarity of conspicuous dark banding or mid-lateral stripe patterns (cf. frequent displays in other species with bright primary stripes). Recently-settled specimens display near-identical colouration to later stages, although less conspicuously.

Lethrinus variegatus Valenciennes

Pl. 3D, Fig. 10

Material examined. (29 specimens: 14–114 mm). AUSTRALIA Great Barrier Reef region, AMS I.32476-004 (2:16 mm), AMS I.34911-011 (1:30 mm), AMS I.34911-012 (1:25 mm), AMS I.34933-001 (2:14 mm), AMS I.34934-001 (2:28–47 mm), AMS I.34935-001 (3:34–35 mm), AMS I.34936-001 (1:32 mm), AMS I.36201-001 (1:15 mm), AMS I.37803-001 (1:16 mm), USNM 336691 (3:26–35 mm), not retained (9:24–69 mm); FIJI Suva, AMS I.22232-016 (1:114 mm); INDONESIA Eastern Archipelago, NMV 46329 (1:73 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-015 (1:38 mm).

Diagnosis. Body slender, body depth 3.1–3.5 in SL; 4.5 dorsal scale rows, 13–14 ventral scale rows; maxillary serrations absent at greater than 23 mm; cheek scales retained until 47–50 mm; dorsal spine 4 the longest.

Diagnostic colour notes. Dorsum finely-mottled grey-tan, seldom with dark banding, dorsal margin of lateral-line off-white; dark mid-lateral stripe semi-permanent, yellowish brown, width approximately 4.0 in body depth, shoulder blotch inconspicuous or absent; ventral half of body abruptly silvery off-white; dark suborbital blotch at greater than 30 mm; fins hyaline.

Pre-settlement colour notes. At 14–16.5 mm (Fig. 10): head and body translucent off-white, melanophores overlying yellow-orange xanthophore pigmentation; distinct dark stripe extending from lips to orbit margin, continuing as dark mid-lateral stripe between posterior margin of orbit and caudal peduncle, may appear as series of irregular blotches; lateral-line cryptic, 3–5 irregular blotches along dorsum, interspaces silver, occasionally 3–6 less-distinct blotches extending below dark mid-lateral stripe from pectoral fin to mid-way along caudal peduncle, further 2–3 irregular blotches adjacent to anal fin; fins hyaline.

Colour notes. A distinctive species with minimal ontogenetic variation following settlement, few differences noted between field and captive or freshly-killed colouration. At 25–50 mm: dorsum and nape finely-mottled grey-tan, 4–6 narrow dark bands above lateral-line and 2–3 similar bands along caudal peduncle, often switched off in field, lateral-line bordered dorsally by silvery off-white interspace in field; yellow-brown mid-lateral stripe extending from lips through orbit to base of upper caudal rays, semi-permanent (cf. intermittent stripe in other species), width 4.0 in body depth, may appear as series of dark blotches in captivity (Pl. 3D), blotch below dorsal spines 3–4 forming diffuse cuboidal shoulder blotch; ventral half of body and head abruptly silvery white, without dark markings in field, often 2–3 diffuse brown stripes or bands between pectoral and anal fins in captivity (Pl. 3D) or after death, 3–4 dark blotches on cheek and operculum from 25 mm; fins mostly hyaline, anterior half of spinous fins with diffuse dark patches over off-white to pale yellow, caudal fin pale yellow with 2–3 indistinct dark bands at greater than 40 mm.

Colour in alcohol. At 25–50 mm, dorsum and nape uniform pale tan; lips and snout with dense melanophores, dark dorsal bands retained though dulled, often connecting with broad blotches on flank, dark mid-lateral stripe identical hue to dorsum, shoulder blotch usually visible; body abruptly off-white ventrally, faintly mottled; fins hyaline, sparse melanophores retained along spines.

Ecology. Moderately common in shallow seagrass beds on lagoonal or fringing coral reefs (*Cymodocea, Halodule, Thalassia*; 0.2–4 m), absent from non-seagrass areas at Green Island at less than 100 mm; solitary when recently-settled (20–40 mm), larger juveniles occasionally join small multi-species schools with congeners, particularly *L. atkinsoni, L. genivittatus, L. harak*, and *L. obsoletus*; observed resting on the substrate among seagrass shoots at night, not fleeing when approached.

Field identification. Distinguished from other *Lethrinus* species by its elongate body and snout profile, and prominent yellow-brown mid-lateral stripe. When observed from behind, may be confused with species such as *L. obsoletus* or *L. genivittatus* on the basis of their similar dark mid-lateral stripes. When freshly collected, particularly at night, may appear a uniform pale olivaceus cream; the dark mid-lateral stripe and shoulder blotch becoming visible after 10–30 seconds.

Previous descriptions. Colour plates of juveniles were included in Kuiter & Debelius (1994) and Kuiter (1996) (size not given in each case), and Lee (1993) (specimen 147 mm, misidentified as *L. semicinctus*).

Lethrinus xanthochilus Klunzinger

Pl. 3E, Fig. 3B

Material examined. (10 specimens: 19–92 mm). AUSTRALIA Great Barrier Reef region, AMS I.34912-007 (1:19 mm), AMS I.34912-008 (1:22 mm), AMS I.34922-001 (1:73 mm), AMS I.34923-001 (1:26 mm), USNM 336684 (1:25 mm), lost (1:48 mm); PAPUA NEW GUINEA Trobriand Islands, AMS I.17102-081 (1:44 mm), AMS I.17099-005 (3:66–92 mm).

Diagnosis. Body moderately deep, depth 2.6–3.2 in SL; 4.5 dorsal scale rows, 15–16 ventral scale rows; maxillary serrations 7 at 18–19 mm, 1–4 (usually 2–3) at 20–28 mm, absent at greater than 28 mm; cheek scales retained until 44 mm; dorsal spine 5 the longest at 18–19 mm, 3 or 4 the longest at greater than 20 mm.

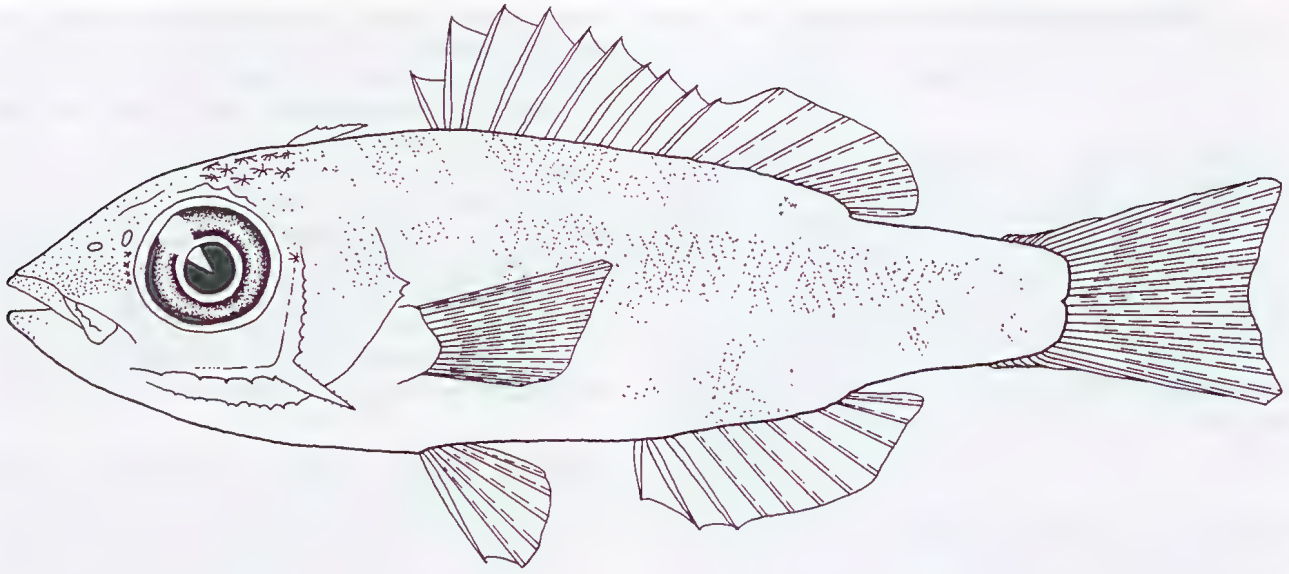

Fig. 10. *Lethrinus variegatus* 13.9 mm SL, late pre-settlement stage. Composite drawing based on AMS I.34933-001 (2 specimens), Green Island. Details of scalation, myomeres and internal pigmentation are not shown.

Diagnostic colour notes. At 18–75 mm, dorsum cream to pale bronze, body abruptly silvery off-white ventrally, silvery off-white interspace along mid-body (22–45 mm) with 2–3 short brown stripes below; black suborbital blotch at 20–45 mm; shoulder blotch inconspicuous; pectoral base scarlet at greater than 50 mm, spinous fins with dense melanophores at greater than 19 mm, appearing black when folded at rest.

Colour notes. A species with distinctive early-juvenile colour patterns which differ markedly from the adult colouration, capable of rapid colour pattern changes. At 18–20 mm, recently-settled: snout, nape and dorsum cream to pale tan, ventral half of head and body abruptly silvery off-white, lateral-line cryptic, prominent silvery off-white interspace along mid-body between cheek and base of caudal rays (Pl. 3E), diffuse grey to brown banding and blotches along body, 4–6 irregular bands forming along dorsum, 2–3 similar bands (or single broad band) on caudal peduncle, usually bisected by mid-lateral interspace; series of 3–4 exceedingly faint grey blotches between lateral-line and mid-lateral interspace, 2 short primary stripes in approximately pectoral and ventral configurations (Pl. 3E, Fig. 3B,4), may fuse below dorsal spines 8–10 and extend onto caudal peduncle as single stripe; diffuse dark markings forming on head as small blotch below orbit, blotches along rear margin of preoperculum and operculum, and band passing through lips; fins mostly hyaline, anterior half of spinous fins with black patches over off-white to yellow, appearing black when folded at rest.

At 20–73 mm (Pl. 3E): background of body gradually darkening with growth to pale bronze dorsum and off-white belly; dark markings on head and body more intense, particularly in field, dark brown to black (Pl. 3E), shoulder blotch more distinct although only at capture or after death, ventral network of indistinct bands joining blotches along lateral-line with belly at greater than 50 mm, 2–3 diffuse bands across snout and nape (Pl. 3E); silvery off-white interspace becoming clearer (20–45 mm) then indistinct (50–73 mm); dark mid-lateral stripe occasionally displayed in field, width approximately 4.0 in body depth, moderately-intense; pigmentation on fins more intense, pectoral fin pale pink at greater than 50 mm, scarlet patch at pectoral base from 50 mm.

Colour in alcohol. At 18–20 mm, body off-white, dark markings on head, body and fins distinct although faded; 21–92 mm (Pl. 3E), dorsum off-white to pale tan, silvery off-white ventrally, dark patterns along body, head and fins distinctly retained, silvery white mid-lateral interspace usually prominent (21–50 mm), red pectoral base (50–92 mm) indistinguishable.

Ecology. Uncommon at Green Island, settlement and nursery habitat preferences uncertain, at 20–73 mm only found over shoreline seagrass cover (0.2–2.0 m; *Cymodocea, Halodule, Thalassia*), specimens 44–92 mm from the Trobriand Islands (Papua New Guinea) collected over sand near patch reefs, 0–1 m; a solitary 35 mm individual at Green Island was noted sheltering amongst epiphytic algae at the base of the seagrass canopy, two 40 mm individuals were noted foraging with congeners (*L. obsoletus* and *L. variegatus*), *Halichoeres miniatus, Lutjanus fulviflamma* and *Siganus fuscescens* of a similar size, fleeing over the seagrass canopy when closely approached; not appearing site attached, other field behaviours unknown.

Field identification. A distinctive species, easily recognised in the field by its prominent silvery white mid-lateral interspace (20–50 mm) and black suborbital

markings. The red patch at the pectoral-fin base may be a reliable character for the field identification of individuals greater than 55 mm, along with the presence of intense black fin pigmentation (but see "Identification note" below).

Identification note. The intense black pigmentation on spinous fins of preserved specimens may lead to confusion with *L. miniatus*. No confirmed juvenile records exist for the latter species on the GBR, although two specimens are known from Sydney Harbour (Australian Museum, I.19103-010 and I.24474-002). Morphological differences distinguishing *L. miniatus* and *L. xanthochilus* at less than 110 mm include a concave interorbital area in *L. xanthochilus* (at greater than 40 mm) (flat or convex in *L. miniatus*), a slight to moderately-humped interorbital margin in *L. xanthochilus* (straight in *L. miniatus*) and deeper body profile of *L. miniatus*.

Remarks. Carpenter & Allen (1989) queried the occurrence of *L. xanthochilus* in Australian waters, although Williams & Russ (1994) noted several records from the central and northern regions of the GBR. The individuals described here represent the first confirmed juveniles to be collected from Australian waters.

Discussion

The juvenile descriptions presented above indicate the occurrence of complex juvenile colour patterns in a suite of 11 *Lethrinus* species from the Great Barrier Reef. In considering the consequences of these patterns to the ecology of *Lethrinus* juveniles, two points are salient. Firstly, each of the three shared colour patterns is associated with a particular suite of behavioural interactions. Secondly, a characteristic feature of *Lethrinus* early juvenile colouration is the degree of interspecific conservatism within each shared pattern.

The first shared pattern, the primary stripes, is notable in that two groups based on this pattern were evident within the species examined; namely species displaying conspicuous and well defined stripes of an orange or pink colour (*L. genivittatus, L. lentjan, L. obsoletus* and *L. ornatus*) and the remainder with inconspicuous stripes of varying hues (as in *L. erythracanthus* and *L. xanthochilus*). Display of primary stripes in the former group is concentrated during incidents of disturbance or when fleeing from aggressors, suggesting them to represent a "fright" or "stress" response. In turn, their ultimate function may be to visually alert other individuals to the presence of danger (Rowland, 1979). A similar explanation may also pertain to species with inconspicuous stripes, although this remains unclear.

The second shared pattern, dominated by the dark mid-lateral stripe, is (a) displayed in undisturbed individuals when schooling or solitary, (b) rapidly disappears in the presence of aggressors, and (c) shows a striking resemblance to similar patterns in juvenile siganids and some mullids and labrids of a similar size. It has been inferred that conspicuous striation in other reef fishes acts to visually confuse piscivores (Barlow, 1972; Ehrlich & Ehrlich, 1973; Bellwood & Choat, 1989). A similar predation-avoidance utility may also apply to this pattern in juvenile lethrinids, particularly given the exposure to predators when swimming or hovering over the seagrass canopy. Alternatively, the correspondence of this pattern with siganid juveniles may indicate it to act as an aposematic model; thereby, conferring a protective advantage through an avoidance by piscivores of siganids and their toxic spines.

The third shared pattern, dark banding, is utilised during antagonistic interactions with conspecifics and congenerics; usually displacing the dark mid-lateral stripe pattern. Such displays are effected through the rapid and contrasting appearance of intense dark banding over a pale background. Conspicuous patterns of this nature have been interpreted as "startle displays", functioning as visual warning or alarm signals (Hamilton & Peterman, 1971; Baylis, 1979). Alternative forms of this pattern in *Lethrinus* juveniles, such as displays of low contrast and intensity, and the appearance of broad bars after dark, probably renders individuals cryptic against the seagrass canopy background (e.g., Barlow, 1972). Both the dark mid-lateral stripe and banding patterns are typified by *L. atkinsoni, L. genivittatus, L. harak* and *L. obsoletus*.

The degree of interspecific similarity seen in *Lethrinus* juvenile colour patterns is not unprecedented among reef fish assemblages. In both Caribbean (Ehrlich & Ehrlich, 1973) and western-Pacific (Bellwood & Choat, 1989) assemblages, such coordination appears associated with multi-species schooling. On the GBR, juvenile lethrinids, siganids, mullids and labrids may all display similar darkly-striped patterns while schooling together over seagrass. The formation of multi-species schools by reef fishes is generally believed to function in predation avoidance (e.g., Ehrlich & Ehrlich, 1973; Hobson, 1978; Wolf, 1985; Bellwood & Choat, 1989). Indeed, schooling over open seagrass near reefs invokes considerable exposure to piscivorous carangids, lutjanids, serranids and synodontids (Baelde, 1990; Blaber *et al.*, 1992; Sweatman & Robertson, 1994; author's pers. obs.). In this environment, lethrinids would undoubtedly benefit from shared patterns through increased signalling efficiency among species, as well as the "disruptive" value of dark stripes.

Similarities in *Lethrinus* juvenile field colouration, and rapid and frequent interchanges between colour patterns, also allude to the problematical nature of identifying small individuals in the field. Although specimens may be conspicuous and easily detected, subtle differences in colour pattern between many species, and their tendency to change patterns when approached, makes lethrinid juveniles difficult for inexperienced observers to separate. Nevertheless, colour patterns represent the most accurate means of identification. Most species can be readily distinguished, particularly if individuals are followed for several minutes to allow their full range of colour patterns to be determined. The *L. lentjan/nebulosus* species pair is exceptional, with separation often tentative or impossible below a minimum size. In other cases, meristic counts and freshly-killed colour patterns from collected material may be used for subsequent confirmation.

Simultaneous investigations of juvenile colour patterns and behaviour may provide an insightful means of increasing our knowledge of early post-settlement regulatory mechanisms and evolutionary history in reef fish populations. Although the capability of comparative studies to identify adaptive traits has been questioned (e.g., Leroi *et al.*, 1994), observations of characters, such as colour patterns, shared between unrelated species may nevertheless yield useful information. Similarities in behaviour and colour pattern between lethrinid and siganid early juveniles are of particular interest in this regard, and worthy of further attention. Juvenile colour patterns and their ontogeny can also contribute valuable information for exploring phylogenetic relationships among reef fishes (e.g., Bellwood, 1994).

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Morphometrics in the Genus *Amenia* and Revisionary Notes on the Australian Ameniinae (Diptera: Calliphoridae), With the Description of Eight New Species

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ABSTRACT. The Ameniinae comprise seven genera, of which six occur in Australia; the largest, *Amenia*, is restricted to this country. Previous studies left some uncertainty about the status of several taxa in *Amenia*, and Part 1 of this study applies morphometric methods to the problem. These analyses show that *Amenia longicornis* comprises two geographically isolated, morphologically distinct forms. One occurs around the head of Spencer's Gulf in South Australia and north as far as Alice Springs; the other is widespread across the Nullarbor Plain. Similar studies of *A. i. imperialis* and close relatives show that *A. i. imperialis* and *A. i. dubitalis* are clearly separable by head shape; also, that two other "forms" of *A. imperialis* can be distinguished: one occurring in northwestern Australia and arid areas of New South Wales and Queensland, the other in the vicinity of Cooktown, Queensland. Likewise, the two subspecies of *A. leonina, A. l. leonina* and *A. l. albomaculata* are morphometrically separable, but with some sign of intergradation, as well as the existence of distinct "forms" of *A. l. albomaculata* in the New England area of New South Wales and on the Eyre Peninsula, South Australia. Finally, *A. chrysame* is shown to comprise two morphometrically separable "forms", occurring north and south of the 26th parallel.

In Part 2, the subfamily Ameniinae is reviewed, with descriptions of eight new species: two in *Stilbomyella*, four in *Paraplatytropesa*, and two in *Amenia*. The last represent morphometrically recognised siblings of *A. imperialis*. Also, the subspecies of *A. imperialis* are raised to full specific rank, as are those of *A. leonina*; genus *Formosiomima* is relegated to synonymy under *Amenia*; the New Guinean *Platytropesa simulans* is newly recorded from north Queensland; and the known ranges of several other species are extended with new records. In Part 3, phenetic studies are offered to support the existing classification within the subfamily, and its zoogeography and possible evolutionary history are discussed. It seems not unlikely that the Australasian taxa stem from a *Paramenia*-like ancestor, that originated in western New Guinea as sister to the mainly Oriental *Catapicephala*. One or more of its descendant species then entered Australia from the north, dispersing, with further concurrent speciation, in a clockwise fashion around the continent.

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The Ameniinae comprise a clearly demarcated group of seven genera that have had a somewhat chequered taxonomic history. Originally placed in Tachinidae (because of the apparent presence of a subscutellum), the studies of Crosskey (1965) have led to a general acceptance that they are best placed in Calliphoridae. Of the seven genera, six occur in Australia and two of these (*Amenia* and *Paraplatytropesa*) are known only from this country. Specimens resemble blowflies, but with metallic colours, often boldly marked with white spots or bands.

In his detailed studies of the subfamily, Crosskey (1965, 1969, 1972) had to leave several questions with rather tentative answers: principally, the taxonomic status of several populations in *Amenia* of which there were too few specimens to allow firm decisions to be made. Since then the material available in Australian collections has grown considerably, as have our facilities for fast and accurate processing of numerical data. Morphometric analyses of adequate material have now provided reasonable answers to some of these questions. At the same time, new and intriguing problems have appeared.

Part 1 of this paper deals with the morphometrics of the populations mentioned, plus a parallel study of a related species. The taxonomic conclusions are formally stated in Part 2, which also includes observations on several other genera of Ameniinae. Finally, in view of our now-abundant information about these handsome flies, I add in Part 3 some numerical studies relevant to the classification of the subfamily and some informed speculation about their zoogeography.

Biology

We still know very little of the biology of the Ameniinae, but the available evidence suggests that all species are macrolarviparous and parasitic as larvae in land-snails. Practically all that is known was summarised by Ferrar (1976). He described the rather distinctive macrolarviparous reproduction of species of *Amenia* and *Paramenia* and collected records of parasitisation of land-snails by species of *Amenia, Paramenia*, and *Formosiomima*. To these I can now add a record for *Silbomyia* and four more for *Amenia* (*imperialis, dubitalis, leonina,* and *longicornis*; see Part 2). Crosskey (1969) also noted that species of *Stilbomyella* and *Platytropesa* are attracted to snails. The parasitic habit helps explain the considerable variation in size that is sometimes observed in ameniines (through truncated development caused by death of the host). It may also help explain some puzzling features in the systematics of the group. At present, the great need is for further rearing, from carefully identified hosts.

Methods and methodology

Ordinations. For morphometric studies, selected characters were measured with a micrometer eyepiece or, in a few cases, scored subjectively. The data were designed for statistical analysis rather than taxonomic description and are not presented here in full. However, copies can be provided by the author on request. Apart from simple statistics, the analyses employed two main techniques: (a) principal component analysis (PCA) of the correlation matrix, i.e., with character vectors normalised by standardisation; components were equally weighted by the option of normalising scores so that their squares sum to unity (my programme COMPAK); (b) multiple discriminant function analysis (MDA), using the canonical variate programme in the GENSTAT package. The use of MDA was entirely heuristic. Significance tests were ignored, because the necessary conditions, of uniform variances, etc., were clearly violated.

A word is in order concerning the application of ordinations to taxonomic studies. An ordination by, for instance PCA, provides a 2-dimensional, visual display of phenetic relations that are discoverable in the data; and, if (for instance) components have been normalised, the relationships depicted owe nothing to the effects of correlation between characters over the whole group. Suites of correlated characters are extracted and equally weighted. On the other hand, well-defined subgroups (if reasonably similar) may appear as parallel, elongate, even linear, clusters, just because of individual, within-subgroup correlations. Devotees of MDA seem sometimes to regard this as damning. Per contra, I find it useful, to confirm the objectivity of the groups to which one is about to apply MDA.

Here, and in ordinations at large, great care must be taken not to read too much into perceived clusters. On their own they can do little more than generate hypotheses that may be worth testing. On the other hand, if one has some independent, external criterion (hypothesis) for forming clusters, patterns on an ordination diagram may provide very satisfying confirmation (or, for that matter, an incongruent pattern, or even absence of pattern may disconfirm the hypothesis). This argument may, of course, be turned around. In the present case I have started with taxonomic hypotheses taken from the literature, and sought confirmatory clustering patterns in the ordinations. However, I have also searched the diagrams for lower-level clusters of specimens that are related geographically or ecologically: this, in the reasonable belief that such correlations are worthy of further scrutiny. In some cases little more could be found; but in others, further characters were then found that confirmed the distinctiveness of a "local" population. This in turn has generated credible hypotheses that help explain the observed patterns.

Measurements used. A suite of 16 male characters was selected, taken from the literature and/or suggested by preliminary testing; as follows:

1 Frons width (*Frw*); the minimum distance between the eye margins.
2 Frons length (*Frl*), from lunula to margin of anterior ocellus.
3 Parafacial width (*Pfw*), at mid-length.
4 Gena width (*Gnw*), from eye-margin to subcranial pit (the latter is seen in lateral view as a small but distinct, pit-like depression near the ventral angle of the triangular epistomal projection).
5 Face length (*Fcl*), measured between the level of the vibrissae and that of the antennae bases.
6 Intervibrissal distance (*Ivb*).
7 Length of antenna (*Ant*), from base of long seta on segment 2 to apex of segment 3.

8 Eye height (*Eyh*), its maximum dimension in half-facial view.
9 Head width (*Hdw*), in facial view.
10 Strength of outer vertical bristle (*Ovb*); scored as 0 for absent and 1–3 for successive degrees of strength (estimated subjectively).
11 Strength of upper orbital bristle (*Uob*), lateral to ocelli; scored as for number 10, but 0-2 only.
12 Wing length (*Wgl*), from humeral crossvein to apex.
13 Distance from angle of vein M1 direct to margin (*AM1*).
14 Costal bow (*Csb*), measured as the maximum displacement of the inner margin of the costa from a line between the apices of subcosta and humeral crossvein.
15 Basal width of the facial carina (*Cwb*), measured between the apices of the second antennal segments.
16 Maximum width of the facial carina (*Cwm*), usually at about two-thirds length.

General. The morphological terminology follows that of Colless & McAlpine (1991).

Many features are illustrated in Crosskey (1965), as are the particular attributes of many species. The computer programmes used are mainly my own, but most well known phenetic packages, such as NTSYS, provide similar facilities.

All holotypes are deposited in the Australian National Insect Collection, as are other specimens unless otherwise specified. Specimens denoted as "examined" are *ipso facto* paratypes unless expressly excluded (ICZN, para. 72b).

Abbreviations for bodily dimensions are given above, for institutes, as follows: AM—Australian Museum, Sydney; ANIC—Australian National Insect Collection, CSIRO, Canberra; QDPI—Queensland Department of Primary Industries; QM—Queensland Museum; SAM—South Australian Museum; UQ—University of Queensland Insect Collection; VM—Museum of Victoria. NP—National Park.

Figure 1. Distributions of forms of *Amenia longicornis* (overlapping records omitted). Filled squares = "eastern form"; filled triangles = "western form"; star = Payne's Find.

PART 1. MORPHOMETRICS

Amenia longicornis (Malloch)

Crosskey (1965) saw only 12 males and four females of this species, but marked variation in several characters was clearly evident. To quote Crosskey: "Male specimens from South Australia have short antennae, a short facial carina which is regularly elongate in facial view, a broader vertex, rather strongly developed outer vertical setae and a strongly marked forward bowing of the costal margin of the wing; most males from Western Australia, on the other hand, have elongate antennae and a long rather lanceolate facial carina, a narrower vertex, very weak or hair-like outer vertical setae and no well marked bowing forward of the costa". On the few specimens available these characters suggested a gradual transition from one form to the other, and Crosskey could only speculate on the possible existence of an East-West cline.

The abundant material now available shows that male (but not female) characters provide a clear geographic division into eastern and western populations (Fig. 1). The former is, as far as known, isolated in the Flinders Ranges and around the head of Spencer Gulf in South Australia, extending north to the vicinity of Alice Springs. The latter occurs across the Nullarbor Plain and has been taken as far east as Nunjikompita (longitude 134°20'E); but is rare or absent between there and Iron Knob in South Australia (longitude 137°09'E). For instance, it was not taken during intensive collecting at Poochera (longitude 134°50'E), whereas numerous specimens were taken a few days later around the head of the Great Australian Bight (longitude ca 131°00'E). To the west, there is a more or less continuous distribution as far as the vicinity of Norseman (longitude 121°50'E), extending south to the coast at Esperance and north to Widgiemooltha; but only 5 specimens are known from areas further north or west. These include an enigmatic specimen from Payne's Find, 500 km northwest of Norseman (see below).

The analyses that follow concentrate, therefore, on possible differences between the isolated populations, and on possible clinal variation on an east-west axis.

In all 54 males were studied. The eastern population was represented by only 8 (3 from Wilpena Pound and 5 from the Whyalla-Iron Knob area)—a meagre sample, but (I believe) sufficient to support the conclusions reached. The western specimens included the holotype (from an unknown locality in Western Australia) and samples of from one to ten specimens from 15 localities covering the known range. In general, sample sizes were so small that MDA was applied only to the East-West contrast.

PCA yielded 3 components that together explained 89% of variation. Examination of scores on component 3 showed that specimens were scattered more or less at random on that axis, so it was considered no further. Component 1, explaining 70% of variance, was an "overall size" component, with most dimensional characters showing substantial loadings of the same sign. Component 2 explained a further 13% of variance, contributed principally by *Ant* and *Fcl* (positive), with

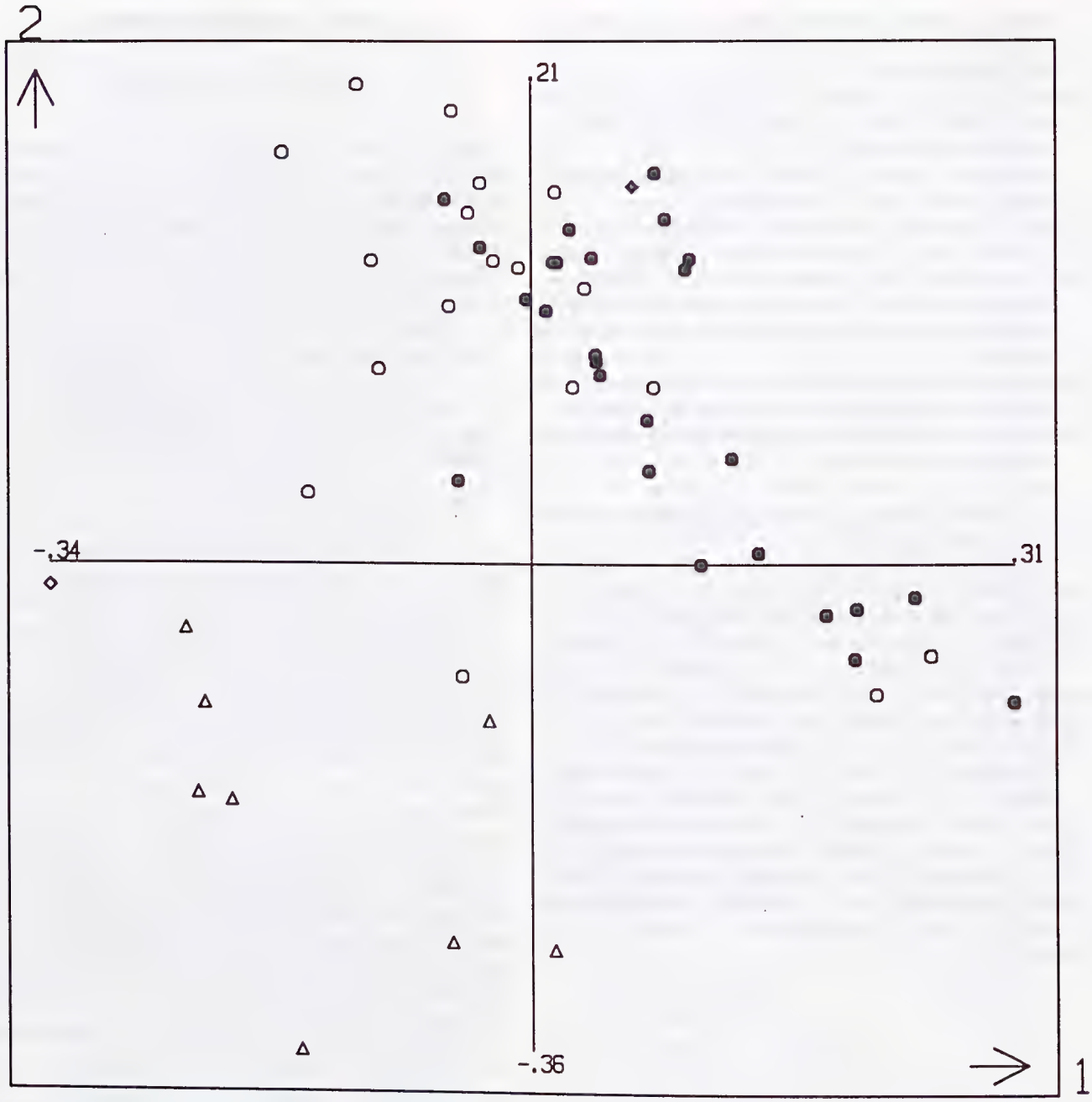


Figure 2. Ordination of 54 male specimens of *Amenia longicornis* on PCA axes 1 and 2. Open triangles = "eastern form"; open circles = "western form" from east of 125°E; filled circles = the same, west of 125°E; filled diamond = holotype; open diamond = Payne's Find specimen.

secondary contributions from *Uob* and *Cwm* (negative). In the ordination shown in Fig. 2, which plots scores on component 1 against those on component 2, it can be seen that eastern and western populations are clearly differentiated on component 2. An exception is a specimen from near Madura, W.A., with an unusually short (perhaps aberrant) antenna, but even it falls outside the envelope of points for the eastern specimens. On component 1, although the eastern specimens tend to be larger, 4 out of 8 fall within the range of the western population. The specimen from Payne's Find, however, is clearly differentiated from all others by its size.

Thus, eastern and western populations are clearly separated by a complex that included 5 of the 6 characters noted by Crosskey; significant variation was not confirmed for vertex width, but was found in one extra character (development of upper orbital bristle). While important, the bristle characters were not crucial. PCA of dimensional characters alone yielded an ordination (not shown) very similar to Fig. 2, with (as expected) component 2 dominated by *Fcl* and *Ant*. Interestingly, the two populations are simply and completely separated by "shape" of the carina, as indexed by the ratio *Cwb*/*Cwm* (Table 1; note that apparent overlap of ranges is due to rounding).

Table 1. Selected ratios and MDA scores discriminating eastern and western forms of *A. longicornis* (8 and 45 specimens respectively). "Payne's Find" specimen shown separately. For abbreviations, see text.

Character	Eastern form		Western form		Payne's Find
	Range	Mean	Range	Mean	
Cwb/Cwm	0.7–0.8	0.77	0.4–0.7	0.61	0.80
(Frw+Eyh-Fcl)/Hdw	0.5–0.5	0.51	0.4–0.5	0.42	0.49
MDA score	3.7–5.1	4.50	-3.2–1.1	0.65	2.40

Finally, MDA showed eastern and western populations to be completely discriminated by a function for which scores are summarised in Table 1. The major loadings were on *Frw* and *Csb*, with smaller but substantial contributions from *AM1*, *Eyh*, and *Fcl* (the last negative, the others positive). MDA thus confirms the significance of the one remaining character (*Frw*) from Crosskey's set. A crude but effective version of the discriminant function is the ratio (*Frw* + *Eyh* - *Fcl*) /*Hdw* (Table 1).

A specimen that has recently come to hand (Palm Valley, MacDonnell Ranges, Northern Territory, 21–22 May 1983, G.A. Holloway; AM) allows prospective application of the MDA function. As might be expected, its measurements conform well with those of the Eastern form.

The Payne's Find specimen is exceptional, in that MDA allocates it to the eastern form. Although in many ways similar to the eastern specimens, it is distinguished by its larger size, intermediate scores on principal component 2 and the discriminant function, and, of course, its immense geographic separation. Its status remains obscure—especially since its two nearest neighbours (from Walyahmoning Rock) are quite normal "western" specimens.

Figure 2 includes a suggestion of differentiation, perhaps clinal, *within* the eastern form (there is an apparent tendency of specimens from the same locality to cluster on component 2). However, there is clearly no suggestion whatever of such a phenomenon in the western form. Note the wide scatter of specimens in the samples from east and west of longitude 125°00. PCA of western specimens alone (not shown) releases them from within-group correlation effects (the linear clustering seen in Fig. 2); and, as expected, they scatter more or less at random on components 1 and 2. That is to say, the variation observed by Crosskey turns out to involve, not a simple cline, but two distinct geographic forms—with, perhaps, clinal variation within one of them. We may add to that the intriguing hint of a north-western population (Payne's Find) that resembles the *eastern*, rather than the western form (Table 1).

Amenia imperialis Robineau-Desvoidy

Crosskey (1965) recognised that *A. imperialis* could be readily distinguished from the very similar *A. dubitalis* Malloch; but, in view of the closeness of that similarity and an apparent separation in their geographic ranges, he preferred to relegate the latter as a subspecies of the former. Accumulated material now shows that the degree of geographic separation is negligible, the range of *A. dubitalis* being almost completely included within that of *A. imperialis* (Figs 3–6). The consequent likelihood that the two are in fact perfectly "good" biological species calls for more detailed study of their morphological distinctness.

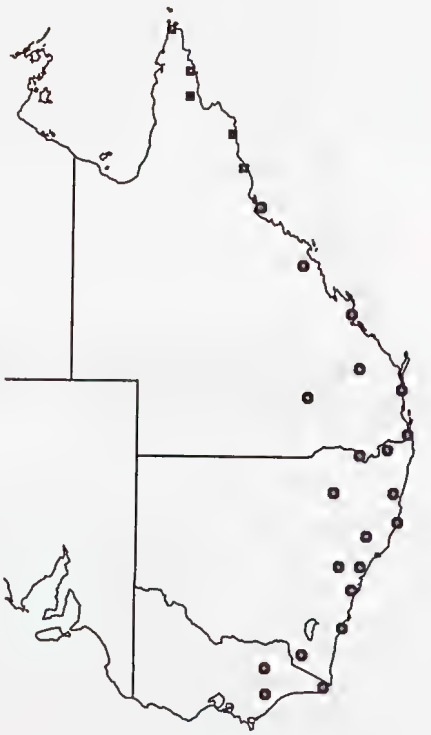


Figure 3. Distribution of *Amenia dubitalis* and *Amenia crinita* (overlapping records omitted). Filled circles = *A. dubitalis*; filled squares = *A. crinita*.

Crosskey's characterisation of the two forms now requires some amendment (see Part 2, below), but his sole dimensional character—the width of frons or vertex—clearly applies. Preliminary tests pointed to correlated variation in other parameters of head shape, although other bodily dimensions showed no sign of significant variation.

The morphometrics of head shape were, therefore, investigated further in a series of 68 males and 63 females, chosen to cover the full geographic range of each taxon as well as a representative range of body sizes. They comprised 20 males and 20 females each of *A. dubitalis* and the "classical" *A. imperialis* (from coast and adjacent mountains), identified by the characters recommended by

Figure 4. Details of recorded distribution of *Amenia dubitalis* in southeastern Queensland and northeastern New South Wales (compare with Fig. 6).

Figure 5. Distribution of *Amenia imperialis* and close relatives (overlapping records omitted). Filled circles = *A. imperialis*; open squares = "arid form"; filled triangles = *Amenia albosquamata*.

Crosskey (1965). The remainder were identified as *A. imperialis*, but came from outlying areas or seemed for other reasons worthy of special scrutiny. In the light of the preliminary tests, 6 dimensions were chosen for measurement: frons width (*Frw*), frons length (*Frl*), gena width (*Gnw*), face length (*Fcl*), eye height (*Eyh*), and head width (*Hdw*). All were measured as described above for *A. longicornis*; this implies that *Frw* was measured towards the middle of the frons in males, but across the posterior ocelli in females.

The close similarity of *A. imperialis* and *A. dubitalis*—and the propriety of analysing them as a single group—was first tested by separate PCA for the 20 *dubitalis* and 20 "classical" *imperialis* males. The 6 loadings on each of the first 3 components from the two analyses (18 paired observations) were almost perfectly correlated ($r = 0.96$). PCA of data for the full set of 68 males then yielded a first, "general size" component explaining 73% of variation. Component 2 explained 18%, with dominant, positive loadings on *Frw* and *Fcl* and negative on *Eyh*. Component 3 explained a further 8%, but provided no obvious taxonomic information and was not considered further.

Figure 7 shows a plot of component 1 against component 2. Not only is *A. dubitalis* clearly separated from *A. imperialis*, but an unexpected pattern of variation is evident within the latter taxon. Two distinct geographic segregates are separated from the main cluster: one comprising six specimens from localities near Cooktown and two from near Cairns, the other including two specimens from the Northern Territory, eight from the Kimberleys (northwestern Australia), and seven from several arid, inland localities in New South Wales and Queensland. I am calling the former the "Cooktown form" and the latter the "Western form" for the present. Other plots (not shown) show quite clearly that the distinction between *A. dubitalis*, the Cooktown form, and other *A. imperialis* is governed largely by the regression of *Frw* on overall size; a similar regression of *Fcl* on size separates the Western form of *A. imperialis* from all the others. For practical purposes, these distinctions are well reflected in the ratios summarised in Table 2.

Accepting the foregoing groupings, MDA (not plotted) confirms that the 4 groups are indeed clearly identifiable. The first discriminant axis explains 80% of variance and, as expected, is dominated by *Frw*; *Gnw* and *Fcl* also have lesser but substantial loadings. The second explains 19%, with its principal loading on *Frl*. There were lesser but substantial loadings on *Frw, Fcl*, and *Eyh* (the first two of these were also prominent on the third principal component). All 4 groups are discriminated on the first axis alone, the second serving mainly to accentuate the distinction between populations of *A. imperialis* from the coastal regions and the "Western form".

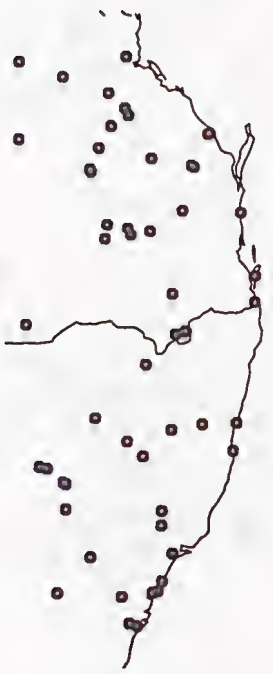


Figure 6. Details of recorded distribution of *Amenia imperialis* in southeastern Queensland and northeastern New South Wales (compare with Fig. 4).

PCA of data for females showed rather similar results, but less clear-cut. The first, "size" component explained 91% of variation; the second explained 4%, with principal loadings on *Frw* and *Fcl*. An ordination on components 1 and 2 (not shown) has the "Cooktown form" mingled with other *A. imperialis*, but specimens of the "Western form" are clearly split off. The remainder form a loose cluster showing a partial separation into *A. dubitalis* and *A. imperialis*.

Further study of the geographic forms of *A. imperialis* revealed that all are distinguishable on additional, qualitative attributes. These are discussed in Part 2 of this paper.

To sum up, *A. dubitalis* and *A. imperialis* are clearly separated, not only by qualitative characters, but also by quantitative parameters of head-shape. Also, morphometrics of *"imperialis"* point to the existence of at least 3 distinct populations. Two are geographically separated, one of them restricted largely to the Northern Territory and Kimberleys, the other to eastern Australia, but with some slight overlap in the interior of New South Wales and Queensland. A third population is everywhere sympatric with the eastern Australian form. The taxonomic implications of these findings are given below in Part 2.

Amenia leonina (Fabricius)

Crosskey (1965), following Paramonov (1957), recognised two subspecies of *A. leonina*, but substituted Macquart's older name *albomaculata* for Paramonov's *enderleini*. Crosskey felt that subspecific status was warranted by the degree of allopatry in the known distributions (*A. leonina* in the north, *A. albomaculata* in the southeast), a feature which has, in this case, held up under the increase of material. Basing my concept of the two taxa on the presence (*albomaculata*) or absence (*leonina*) of at least one median marginal bristle on abdominal tergite 3, plus certain male attributes discussed in Part 2, their currently known distributions are shown in Fig. 8.

To examine any correlated morphometric differences, I selected 50 male specimens of each taxon (as identified by the bristle character) and measured *Frw, Hdw, Eyh*, and *Gnw* (as defined above); also the maximum width of the eye in half-facial view (*Eyw*) and the length of wing-vein R_{4+5}. PCA of the six dimensions showed a fairly clean separation of the two taxa, but with a few highly anomalous specimens from both. There were also signs of the existence of yet another form, represented by several specimens from Eyre Peninsula, South Australia. The PCA results were based mainly on general size and *Frw*, which together accounted for 92% of variation.

A second, more extensive study was therefore made, using all available males—205 in all—and a reduced character set. The latter comprised *Hdw, Frw*, and (as a more easily measured, non-head character) the distance between the posterior pair of dorsocentral bristles (*Pdc*). PCA of the three dimensions yielded a first, "size" component on which the two taxa were distributed apparently at random and which took up only 58% of variation. However, components 2 and

Table 2. Ratios (ranges and means) of selected dimensions of *Amenia dubitalis* and forms of *A. imperialis*. Numbers of specimens in brackets.

Ratio	*dubitalis* (20)	*imperialis*		
		"Eastern" (24)	"Cooktown" (7)	"Western" (17)
Frw/Fcl	0.3–0.4, 0.39	0.5–0.7, 0.60	0.5–0.5, 0.48	0.6–0.8, 0.67
Frw/Hdw	0.3–0.4, 0.33	0.4–0.6, 0.51	0.4–0.5, 0.42	0.4–0.7, 0.53
Fcl/Hdw	0.6–0.8, 0.65	0.6–0.7, 0.68	0.6–0.7, 0.67	0.8–0.9, 0.84
Fcl/Eyh	0.5–0.6, 0.52	0.5–0.6, 0.57	0.5–0.6, 0.54	0.7–0.7, 0.70
Gnw/Eyh	1.0–1.3, 1.13	1.0–1.2, 1.10	1.0–1.1, 1.08	0.7–0.9, 0.82

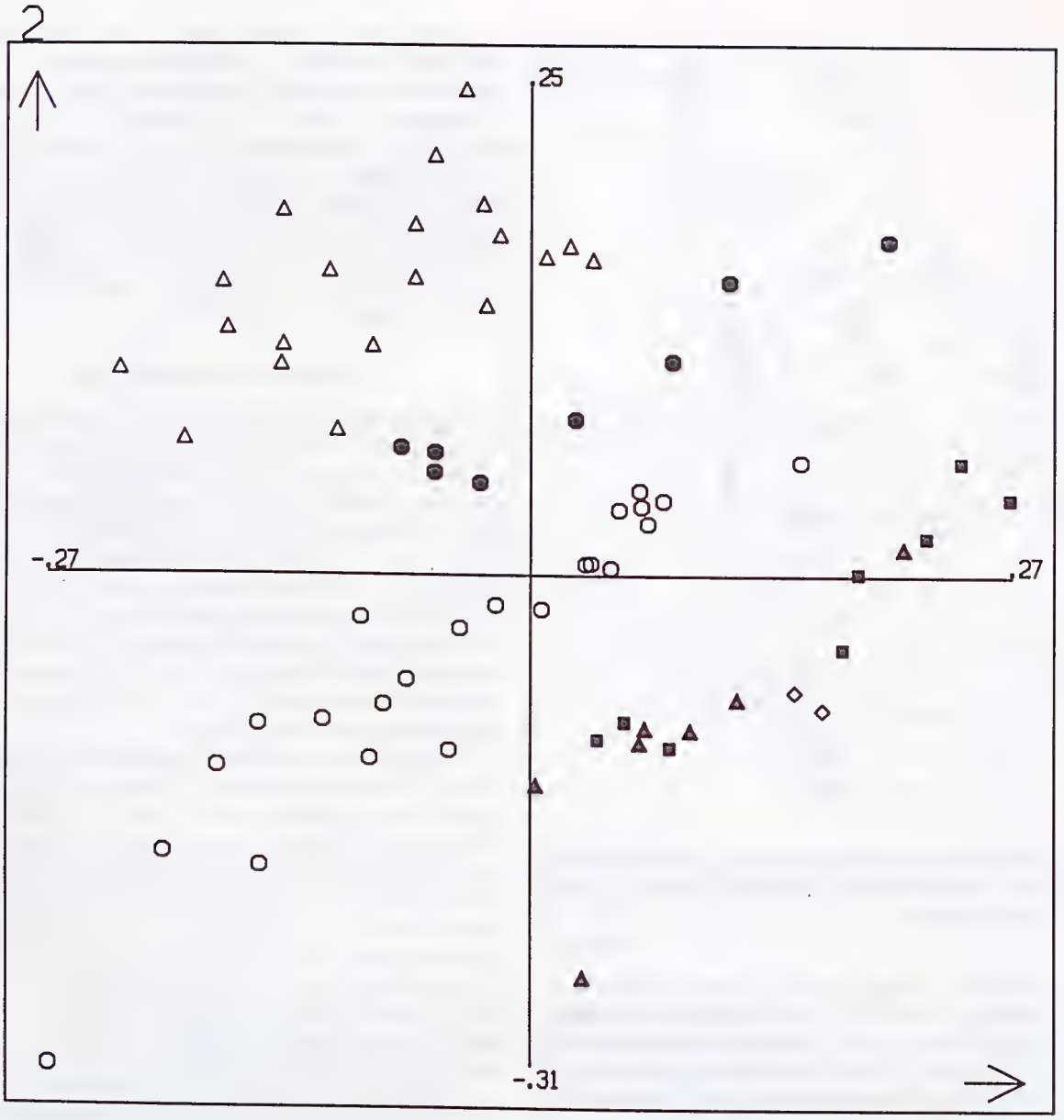


Figure 7. Ordination of 68 males of *Amenia imperialis* group on PCA axes 1 and 2. Open triangles—*Amenia dubitalis*; others—"forms" of *Amenia imperialis*: open circles—typical form; filled circles—Cooktown form; filled squares—western form, Kimberleys; filled triangles—western form, NSW and Queensland; open diamonds—western form, Northern Territory.

3 (with 35% and 7% respectively) were more informative. Component 2 was dominated by *Frw*, and component 3 by a contrast between *Hdw* and *Pdc*. In view of this, and the small number of characters used, the ordination is more clearly presented (Fig. 9, p. 94) as a simple plot of *Frw* against *Hdw*, both scaled by division by *Pdc*. MDA (not shown) gives a very similar result.

Figure 9 demonstrates that "normal" *A. albomaculata* and *A. leonina* are quite well separated by relative head width alone. Frons width serves mainly to distinguish certain exceptional populations of *A. albomaculata* (Fig. 9: "New England" and "Southern" forms). Nor does this reflect any north-south, clinal type of variation. Within each taxon, and omitting the exceptional populations, there is no detectable correlation between normalised head width and latitude.

Another five exceptions are noted on Fig. 9, p. 94: four cases of *A. leonina* with dimensions typical of *A. albomaculata* and one of the converse. These "aberrant" specimens all come from the main area of overlap between *A. leonina* and *A. albomaculata* in southeastern Queensland. In Fig. 9, the 5 "marginal" specimens of *A. albomaculata*, near the centre of the plot, with dimensions close to those of *A. leonina*, also come from the vicinity of Brisbane. On the other hand, 5 other specimens from near Brisbane fall in the main body of the *A. albomaculata* cluster, and are perfectly typical members of that taxon. The same is true of 6 specimens from Noosa, a little north of Brisbane. Also, a further 13 specimens, all collected in the vicinity of Brisbane, came to hand later and were plotted in the foregoing

Figure 8. Distributions of *Amenia albomaculata* (triangles) and *Amenia leonina* (circles) (overlapping records omitted).

fashion. Seven *A. albomaculata* would all fall in the appropriate area of Fig. 9, but only 3 out of 6 *A. leonina* would do so; the other 3 would fall in the *A. albomaculata* area.

The simplest explanation of those observations is that some degree of hybridisation is occurring between *A. leonina* and *A. albomaculata* in the general vicinity of Brisbane, with head shape and the bristle character segregating independently in the hybrids. Nonetheless, if such hybridisation is possible it becomes difficult to explain how outliers manage to persist—such as the male *A. albomaculata* from Mackay, deep in the home range of *A. leonina*, and the 4 female *A. leonina* from Sydney.

These results are further discussed in Part 2.

Amenia chrysame (Walker)

Like the several preceding species, *A. chrysame* has a wide distribution in eastern Australia (Fig. 10). To test whether it, too, might display significant geographic variation, a preliminary analysis was made of 6 measurements and 4 bristle characters on a small set of specimens. This suggested that frons-width (*Frw*, as defined above) does, indeed, vary geographically. The ratio *Frw/Pdc* was therefore measured on 100 specimens, selected to cover the species' range. The ratio proved to have a highly significant regression on latitude ($p<0.01$). However, a scatter-plot (Fig. 11) shows that the regression reflects, not a regular cline, but an abrupt shift in average frons width at about 26 degrees south. Separate analyses of specimens from north and south of the 26th. parallel show no significant regression on latitude. However, the mean frons ratios were 0.27 and 0.20 respectively—a difference that, although small, is statistically highly significant ($p<0.01$ for *t*-test).

On present evidence, I would interpret this as simple geographic variation; but the reason for its occurrence is not at all obvious. Perhaps it reflects some ancient physiographic discontinuity that has long since disappeared—indeed, perhaps the same one that gave rise to *A. leonina* and *A. albomaculata*. The matter is further discussed in Part 3.

Figure 11 shows several other interesting features: (a) a deficiency of specimens with relatively narrow frons in places between 28 and 31 degrees south; (b) an apparent surplus of such specimens in places between 26 and 28 degrees south—i.e., in the general vicinity of Brisbane; (c) a deficiency of specimens with relatively wide frons in places between 31 and 35 degrees south. If these represent more than fortuitous statistical fluctuations, I am at a loss to explain them.

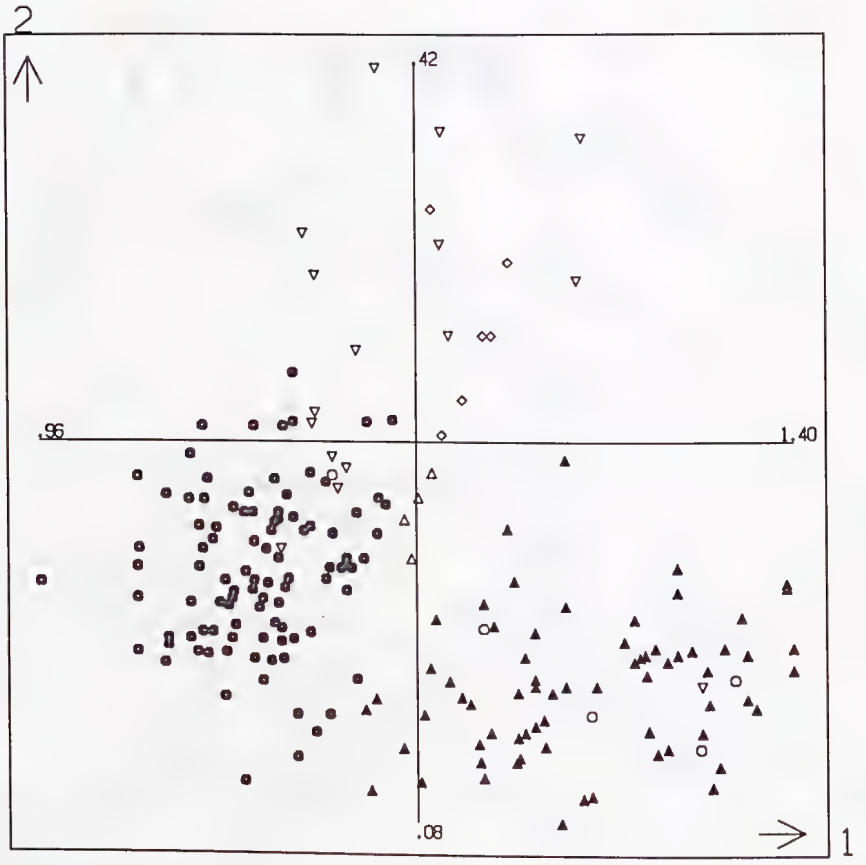


Figure 9. Ordination of 98 males of *Amenia albomaculata* and 107 of *Amenia leonina*; axis 1—*Hdw/Pdc*; axis 2—*Frw/Pdc*. Filled circles—*leonina*; filled triangles—*albomaculata*; open circles—"aberrant" specimens (see text); open triangles—*albomaculata* "marginal" specimens (2 coinciding; see text); open reversed triangles—"New England form"; open diamonds—"Southern form".

Figure 10. Distributions of *Amenia chrysame* (circles), *Amenia nigromaculata* (triangles), and *Amenia sexpunctata* (squares) (overlapping records omitted).

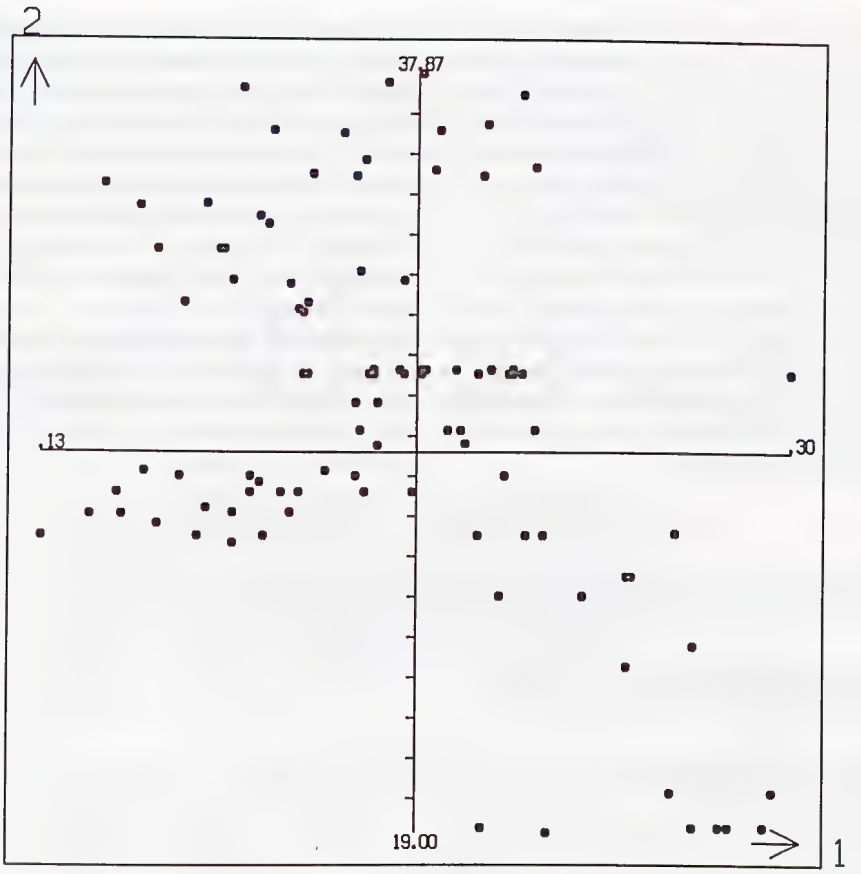


Figure 11. Scatter-plot of 100 specimens of *Amenia chrysame*; axis 1—*Frw/Pdc* (see text); axis 2—latitude (midline marked in degrees).

PART 2. FORMAL TAXONOMY

In this section I formalise the taxonomic decisions foreshadowed in the section on morphometrics and also describe several new species that have come to hand, together with new records and occasional notes on other species. "Specimens examined" are listed only for new species and diagnoses are left to be inferred from the keys. Original descriptions and synonymies are not cited, since they were more than adequately handled by Crosskey (1965, 1969, 1972) and have been recently collated by Kurahashi (1989).

Subfamily AMENIINAE

The diagnosis given by Crosskey (1965) will serve generally to identify Ameniinae:

Calliphoridae with usually metallic coloration; posterior spiracle with cluster of strong hairs on anterior lappet; thorax with weak but distinct development of a subscutellum; head almost always with conspicuous facial carina; postabdomen of female not forming an extensible telescopic ovipositor. And, as secondary attributes: eyes bare; parafacials bare; arista long-plumose; subalar bulla bare; lateral declivity of postalar callus densely long haired; prosternum strongly haired (except in some *Paramenia* spp.); prostigmatic seta present; prothoracic spiracle dark brown; stem-vein of wing bare; vein M bent angularly forwards; hind tibia with strong apical *pv* bristle (except in Parameniini); abdominal sternites very broad and exposed, in female almost always with spinous setae; male terminalia as in Calliphorinae (several other attributes mentioned by Crosskey no longer apply).

To these may be added the presence of infrasquamal setulae on the thoracic mediotergite and the (often) swollen gular area of the head. The last may not always be obvious, but (except in *Amenia* spp.) it is normally detectable. It appears to be absent in other Calliphoridae. The shape of the posterior spiracle is also distinctive; the lappets are roughly equal in area and the posterior one has a smoothly rounded anterior margin and no setulae on the disc (except in some *Catapicephala* spp.). However, the most useful subfamily attribute is still the presence of a tuft of long, dark hairs with fine, "wavy" tips on the anterior lappet of the spiracle. Other calliphorids—e.g., *Chrysomya*—may have a rather similar condition, but the hairs are more normal, not converging into an anterior tuft, and they extend across the posterior lappet as well. Species of *Paraplatytropesa* are a problem, since they may have the lappet hairs weakly, and sometimes not at all, developed; but such specimens may be recognised by the metallic colour, small size, vibrissae level with epistome, parallel inner vertical bristles, and the very prominent swelling of the gular region of the head.

The mainly Oriental genus *Catapicephala* Macquart is now placed in the Ameniinae (Kurahashi, 1989) (see also below, under Parameniini). One species occurs in western New Guinea but none in Australia. *Catapicephala* spp. have the anterior lappet of the posterior spiracle more or less uniformly setose, the length of the hairs varying somewhat between species and sexes. In one female examined, of *C. ingens* (Walker), the hairs were quite sparse and short, but a male of *C. splendens* had them more resembling the ameniine norm, albeit rather inconspicuous. However, the shape of the lappets conforms closely to the rather distinctive form typical of Ameniinae (see above). The subscutellum is also quite well developed, more so, in fact, than in most ameniines. All in all, then, I see no reason to exclude the genus from that subfamily.

I shall refer below to two additional metric characters not employed in Part 1: (a) the relative distance of the bend of wing-vein M to the wing-margin, formalised as the *M-bend index*: the minimum distance from the bend of M_{1+2} to the margin, divided by the distance from the mid-point of the bend to the junction with *i-m*; (b) the *antennal segment ratio*, which is the ratio of the length of antennal segment 3 to that of segment 2, both measured from the junction of those segments on the mesad surface.

Additional species described below necessitate some pruning of Crosskey's (1965) key to genera, to remove attributes that no longer hold good. The following version will serve to identify the vast majority of specimens, if in reasonable condition.

Key to the tribes and genera of Ameniinae

1 Head without any strong facial carina between antennae. Hind tibia without definite *pv* apical spine (Tribe Parameniini) 2

—— Head with strong facial carina separating antennae. Hind tibia with *pv* apical spine (Tribe Ameniini) 3

2 Vibrissae set well above level of epistoma, the latter strongly protruding. Male with eyes approximated at vertex and lacking fronto-orbital bristles ..... *Paramenia* Enderlein

—— Vibrissae set level with epistoma, the latter flat, truncate, and not at all protruding. Male with fronto-orbital bristles and with eyes well separated at vertex ..... *Catapicephala* Macquart

3 Ocellar setae undifferentiated. Thorax without silver patches on humeri and notopleura. Propleural setulae lacking. Female with strong but normal setae on abdominal S2–4 ..... *Stilbomyella* Malloch

—— Head with one or more pairs of clearly differentiated ocellar bristles. Thorax with silvery patches on humeri (except in *Platytropesa* and some *Amenia*). Propleuron setulose (except in some *Paraplatytropesa*). Female with strong spine-like setae on abdominal S2–4 4

4 Ventral surface of costa setulose between apices of Sc and R_1. Scutellum with a pair of strong, erect, often spiniform preapical setae. Frons of male broad, as wide as that of female. Male with strong outer vertical, prevertical and proclinate fronto-orbital bristles, as in female (male not known for *minor*) ..... *Silbomyia* Macquart

—— Ventral surface of costa bare between apices of Sc and R_1. Scutellum usually without erect preapical bristles. Male eyes sometimes strongly approximated. Male sometimes lacking fronto-orbital bristles 5

5 Gular region of head often swollen, conspicuous in profile. Scutellum with 6 marginal bristles. Suprasquamal ridge bare. Crossvein r-m placed at about middle of discal cell. Abdominal T3 and T5 usually without lateral pale spots (except in *Paraplatytropesa argentea*). T4 with up to 8 posterior bristles on dorsal and lateral margins (excluding the smaller slightly ventral ones). Male usually with conspicuous long hairs on abdominal S2 and S3 6

—— Gular region of head at most inconspicuously swollen. Scutellum usually with more than 6 marginal bristles. Suprasquamal ridge usually with group of tiny setulae adjacent to scutellum. Crossvein r-m placed basal to middle of discal cell. Abdominal T3 and T5 almost always with lateral pale spots. T4 with 10 or more bristles posteriorly on dorsal and lateral margins. Male with short, spiny bristles on abdominal S2 and S3 ..... *Amenia* R.-Desvoidy

6 Facial carina conspicuously flattened on anterior surface, separated from epistome by sharp, V-shaped notch. Vibrissae set well above level of epistoma. Hairs of upper occiput pale; genae with pale setulae. Gular region not conspicuously swollen. Mesothorax with at most a trace of silver pruinosity behind humeri ..... *Platytropesa* Macquart

—— Facial carina more or less rounded on anterior surface, sometimes separated from epistome by rounded notch. Vibrissae about level with margin of epistoma (except in *Paraplatytropesa argentea*). Hairs of upper occiput dark; genae with at least a few dark setulae. Gular region conspicuously swollen. Mesothorax with silver pruinosity anteriorly, and over humeral, notopleural, prealar and subalar areas ..... *Paraplatytropesa* Crosskey

Tribe Ameniini

Diagnostic attributes are given in the key to genera.

Genus *Silbomyia* Macquart

The genus is largely Oriental, distributed from India and China to Timor. In Australia, one species (*S. minor*, known from a unique female) is recorded from north Queensland and one (*S. palpalis*, known from 3 males) from northwestern Australia. The genus does not seem well characterised, but I have too little material to attempt a revision.

Silbomyia palpalis Crosskey

I have seen one additional specimen, from the same general area as the type-locality: "W. bank of Turner R. above Kunagunarrina Pool, S. of Port Hedland, W.A., 25 June 1980, B. Duckworth. Map. Ref. = Marble Bar SF50-8-344:155" (AM). It was reared by the collector from a snail, a species of "Quistrachia" (*ms* name).

For the 3 known specimens, the M-bend index (as defined above) is 2.3–4.0.

Genus *Stilbomyella* Malloch

The genus was hitherto known from the Moluccas to New Britain. As predicted by Crosskey (1965), it does occur in Australia as well, and I describe below two new species from North Queensland. One closely resembles the New Guinean *S. gloriosa* (Walk.) (= *S. nigrocostalis* (Doleschall), synonymy by Kurahashi (1989)). The other is more distinct, but is, I think, best placed in this genus.

Stilbomyella crosskeyi n.sp.

Holotype: male; 15°47'S 145°14'E, Shiptons Flat, Queensland, 18 October 1980, D.H. Colless, (at light). ANIC No. 6151. The locality is a little south of Cooktown, north Queensland.

Other specimens examined. QUEENSLAND. 4♂♂, same data as holotype, but coll. 19 October 1980. Coomera River, Lamington NP, 1200 ft, 28 May 1966, Z. Liepa, 1♀. NEW SOUTH WALES. 28°42'S 153°17'E, 1 km E Mt Warning, 500 m, 22 November 1976, I.F.B. Common & E.D. Edwards, 1♂. The last two specimens are not paratypes.

Very similar to *S. gloriosa*, as described by Crosskey (1965; as *nigrocostalis*), but differing as follows:

Male. *Body length* 6.8–8.8, mean 7.5 mm (6 specimens). *Head*. Carina (in frontal view) slightly "pinched" above epistome, sides parallel or slightly tapering ventrally on ventral half, a little longer than lunula to anterior ocellus. *Gnw* 0.4–0.5 of *Eyh*, mean 0.43 (7 specimens) (two New Guinea *gloriosa* average 0.48). Antennal segment 3 relatively short, 0.3 of *Hdw* (two New Guinea *gloriosa* average 0.2), usually at most a little shorter than arista. *Thorax*. Propleuron bare. *Wing*. M-bend index 0.8–0.9. *Legs*. Mid tibia with only 1 strong *ad*. *Abdomen*. T3 and T5 with conspicuous pale silvery spots laterally on the ventrally curved part of the tergite. *Genitalia* very similar to those of *gloriosa* (Crosskey, 1965: fig. 37), but cerci distinctly longer than surstyles.

Female. Secondary sexual differences as for *gloriosa*. Otherwise resembling the male (but see below).

Notes. The above refers to specimens from the type

locality. Another male from Mt Warning, New South Wales, has A3 much shorter, only 0.2 of *Hdw*, and therefore much shorter than the arista (as in *S. gloriosa*), and 2 strong *ad* on the mid tibia. A female from Lamington NP has the same features. Both, however, have the conspicuous pale spots on T3 and T5 that provide the most striking difference from *S. gloriosa*, and I am tentatively placing them as *S. crosskeyi*.

Stilbomyella anomala n.sp.

Holotype: female; Palmerston NP, 1200 ft, Queensland, 18 April 1971, D.A. Duckhouse, (light trap). Ex spirit via ethyl acetate. ANIC No. 6143. The type locality is near the Palmerston Highway, between Innisfail and Millaa Millaa, north Queensland.

A small dark species, body length 7.0 mm.

Female. *Head*. Interfrons dark brown; parafrontals, parafacials, genae, and postorbits golden pollinose; hairs of genae pale golden. In facial view inner surface of facial ridge dark, continuing as a black line through vibrissa and ventrally along subcranial margin. Frons relatively narrow, 0.2 of head width. Vertical bristles strong, inner verticals decussate, parafrontal with 2 strong proclinate fronto-orbitals and 1 exclinate (prevertical); ocellar bristles not differentiated. Carina in lateral view quite strongly protruding, curved; in facial view, more or less parallel-sided on ventral two-thirds, tapering dorsally; separated from epistome by a distinct but rounded notch. Antenna completely dark; segment 3 a little shorter than carina and than arista. Palps dark. Gena 0.4 of eye height. *Thorax*. Scutum and scutellum metallic green, the former (in glancing light) with trace of silvery frosting on humeri and notopleura, and (in some lights) an ill-defined median dark vitta. Scutellum with preapical bristles rather erect (but not "spiny", as typical of *Silbomyia*). Pleura metallic green with large silver-pollinose area over anepisternite and sternopleuron. Propleuron bare. *Legs*. Fore tibia with 1 *pv*, no *pd*. Mid femur with usual group of 3 strong *a* bristles near centre; mid tibia with 2 strong *ad* and 1 *pv*. Hind coxa bare on posterodorsal surface. *Wing*. Costa setulose ventrally between Sc and R_1, as in *Silbomyia*, but not apical to R_1. Membrane strongly infuscated anterobasally, as far back as R_{4+5}, and along M_2 and M_4. M-bend index 0.7. Lower calypter dark on apical half. *Abdomen*. T1+2 dark, other tergites metallic green with apical dark bands in some lights; T3 and T5 with lateral silver-pollinose spots ventrally. T3 with single strong median bristle (presumably an aberration). Sternites dark, with sparse, coarse bristles.

Male unknown.

Notes. Despite the setulose ventral surface of the costa (a "key-character" for *Silbomyia*), *anomala* seems best accommodated in *Stilbomyella* by virtue of the attributes given in the key, especially the unusual lack of differentiated ocellar bristles. As shown in Part 3 (Figs 18–22), it clusters closely with that genus phenetically.

Genus *Platytropesa* Macquart

The genus was known from 3 very similar species variously distributed in the Moluccas, New Guinea, the Bismarck Archipelago and North Queensland. One more of these is here recorded from Australia.

Key to species of *Platytropesa*

1 Anepisternite metallic, without large white pollinose spot (Bismarck Archipelago) ..... *Pl. dubia* (Malloch)

—— Anepisternite mostly covered by large white pollinose spot 2

2 Inner eye margin in facial view slightly but distinctly angulate at about level of lunula. Lower calypter with dark marginal colour extending very distinctly on to the membrane, and continuing around posteroexternal angle. Sternopleuron with at most a trace of pale pollinosity, forming a vaguely defined pale area. Fore-tibia usually with 2 *pd* bristles. Male with 2 pairs of proclinate fronto-orbital setae. Male S5 with very long hairs, their apices conspicuously curved downwards and inwards ..... *Pl. auriceps* Macquart

—— Inner eye margin in facial view evenly curved, not at all angulate. Lower calypter with dark marginal colour extending at most weakly on to membrane, very slightly or not at all continuing around posteroexternal angle (Australian specimens only). Sternopleuron with distinct pale pollinose spot (Australian specimens). Fore-tibia usually with only 1 *pd*. Male without proclinate fronto-orbital setae. Male S5 with shorter hairs, their apices not conspicuously curved downwards and inwards ..... *Pl. simulans* Crosskey

Platytropesa auriceps Macquart

Crosskey (1965) gives a very detailed description. I give below the salient features, and some others not mentioned by Crosskey.

Male. *Head* in facial view with inner eye margins strongly diverging and distinctly angulate at about the level of lunula. Carina strongly developed, its anterior surface flattened, tapering strongly in upper third towards lunula. Parafacials projecting to form deep foveae in which lie the enlarged antennae. Parafrontal with exclinate prevertical bristle and two proclinate fronto-orbitals; also, numerous black setulae and sometimes several pale ones anteriorly. Interfrons very dark brown, the dark setulae of parafrontal extending on to a marginal strip, but at most a short way on to the disc. Palp dark brown. *Mesonotum* emerald green with variable, usually strong, cupreous hue in glancing lights. Sternopleuron with at most a little pale pollinosity, forming an indistinct pale spot in some lights. *Wing*. M-bend index 0.9–1.3. Calypter with dark marginal colour extending on to membrane as a distinct band, covering some 10–20% of the exposed surface and extending clearly around the posteroexternal angle. *Fore tibia* with 1–2 *p* setae, 1–3 *pd* (usually 2); mid tibia with 2 large *ad*, 1 large *v*, 2 medium *p*, and 2–3 small *pd* setae. *Abdominal venter* with conspicuously long and dense hairs, those on S5 with apices strongly curved downwards and inwards (Crosskey, 1965: fig. 30). *Genitalia* as described by Crosskey (1965: figs 39, 42); cerci in lateral view gently curved, their tips rounded; surstyli more or less parallel-sided, their apices about level with those of cerci.

Female. Generally similar to male, differing as follows:

Angulation of eye margin often less distinct. Carina less strongly flattened anteriorly, tapering regularly towards lunula. Antennae shorter, lying in shallower foveae. Parafrontal setulae much less profuse. Abdominal sternites with spinous setae instead of long hairs.

Distribution. Queensland: Palm Island, Etty Bay, Yungaburra, Kuranda, Cairns (Earl Hill, Ellis Beach), Cooktown (Shiptons Flat, Gap Creek), Iron Range.

Platytropesa simulans Crosskey

Crosskey (1965) gives a detailed description of New Guinean specimens. I now have Australian specimens, which differ from *Pl. auriceps* as follows:

Male. Inner eye margin smoothly curved. Parafrontals without proclinate fronto-orbital bristles, with more pale setulae anteriorly. Palp usually pale brown, at least apically. Sternopleuron with quite distinct pale pollinose spot, visible in most lights. M-bend index 0.8–0.9 (i.e., slightly, but distinctly less than in *auriceps*). Calypter with dark colour almost completely confined to margin, scarcely if at all extending around posteroexternal angle. Abdominal S5 with hairs less profuse and rather straight, not conspicuously curved. Cerci more or less straight, slightly hooked at apices; surstyle as described for *auriceps*.

Female. Differs from *auriceps* in shape of inner eye margins, palp colour, pale spot on sternopleuron, and darkening of calypter—though differences not as pronounced as in male.

Distribution. The Australian form is known only from the Iron Range area of Cape York Peninsula.

Notes. There are some quite marked differences between the specimens described above and Crosskey's original description of *Pl. simulans*. These are confirmed by my examination of a female paratype. New Guinean specimens have a much more extensively darkened lower calypter and much less pollinosity on the sternopleuron. The male surstyli of Australian specimens also differ from Crosskey's description and his figures 38 and 41, in more resembling the condition shown for *Pl. auriceps* in his figs 39 and 42. Crosskey does, though, use the term "usually", suggesting that he observed some variation from the shape described.

A case could be made for describing the Australian form as a distinct species; but since it is clearly the local representative of *Pl. simulans*, I am content for the present to leave it under that name.

Genus ***Paraplatytropesa*** Crosskey

The genus was previously known only from a single Australian species. The discovery of additional species (total now five) necessitates changes to Crosskey's (1965) diagnosis of the genus: only two species with carina as described by him (see below); facial ridges sometimes with setae only near the vibrissae; vibrissae set at least a little above the level of epistome margin in 3 species; frons relatively narrow in 1 species; male lacking orbital bristles in 1 species; fore tibia occasionally with a *p* seta (two species); mid femur with more than 1 strong *a* bristle in two species; hind coxa often setulose on posterodorsal surface; abdomen with lateral pale areas on T5 in 1 species. In addition, hairs on anterior lappet of posterior spiracle (diagnostic of Ameniinae) often small, sparse, and inconspicuous, occasionally absent. Despite these deficiencies, the genus remains distinctive, and recognisable by the attributes given in the key. In all but *argentea* the bend of vein M is relatively remote from the wing margin, with index 1.5–3.0.

It is also noteworthy that, with one exception, the female antennal segment 3 is only some 60-75% the length of that of the male—as in *Platytropesa*. *Paraplatytropesa grandicornis* has them of equal length, as in *Stilbomyella*. Also, all but one species have strongly developed bristling on the abdominal sternites, reminiscent of the condition in *Platytropesa* and *Stilbomyella*. In the exception, *Paraplatytropesa argentea*, both male and female have spines on the sternites, as in *Silbomyia*.

Key to species of *Paraplatytropesa*

1 Parafacials golden. Vibrissae set well above level of epistomal margin. Abdominal T5 with lateral silvery spots. Inner vertical bristles strongly converging, decussate ..... *Paraplatytropesa argentea* n.sp.

—— Parafacials silver. Vibrissae set at most a little above level of epistomal margin. Abdominal T5 without lateral silvery markings. Inner vertical bristles not converging, usually more or less parallel (in undamaged specimens) 2

2 Carina narrow, not confluent with epistome. Protruding portion of lower calypter dark. Facial ridges with setulae confined to region adjacent to vibrissae. Abdominal T3 with conspicuous pale areas laterally 3

—— Carina broader, confluent with epistome. Protruding portion of lower calypter pale. Facial ridges with setulae continuing over 50% or more of length. Abdominal T3 without conspicuous pale areas laterally 4

3 Carina pale golden, strongly convex and protruding in lateral view. Genae pale golden. Vibrissae about as long as arista, not strongly decussate. Propleuron bare. Male with frons narrow, "waisted", narrowest in front of ocelli, without strong fronto-orbitals; antennal segment 3 about half as long as head width ..... *Paraplatytropesa parvifrons* n.sp.

—— Carina dark brown, not protruding. Genae pale silvery. Vibrissae much longer than arista, strongly incurved, decussate. Propleuron setulose. Male with broader frons, narrowest across ocelli, and with 2 strong recumbent fronto-orbital setae and 1 reclinate; antennal segment 3 about one quarter as long as head width ..... *Paraplatytropesa grandicornis* n.sp.

4 Genae pale golden. Fore tibia with a *p* seta. Posterodorsal strip of hind coxa bare. Male with profuse long hairs on abdominal S3 ..... *Paraplatytropesa rieki* Paramonov

—— Genae pale silvery. Fore tibia without a *p* seta. Posterodorsal strip of hind coxa often setulose. Male abdominal S3 with only 4–6 long hairs ..... *Paraplatytropesa tropicalis* n.sp.

Paraplatytropesa rieki (Paramonov)

Crosskey did not mention the profuse setulae of the propleuron (not present in some other species). Also, the abdominal sternites have profuse long hairs, not just "a few". The male genitalia are shown in Fig. 12; note the very short surstyles, which barely project beyond the lateral lobes of T9.

I have two additional specimens, also from central Queensland (Bundaberg, March 1973, and Bin Bin Range, west of Biggenden, December 1974, both coll. H. Frauca).

Distribution (Fig. 26, p. 108). Queensland: Palm Island, Springsure, Collinsville, Bundaberg, Biggenden.

Paraplatytropesa parvifrons n.sp.

Holotype: male; 53 km NE of Alice Springs, Northern Territory, 6 October 1978, D.H. Colless. ANIC no. 6150.

Other specimens examined. NORTHERN TERRITORY: 3♂♂ as for holotype; 1♂, 1♀, as for holotype, but 7 October 1978; 39 km E of Alice Springs, 6 October 1978, 1—all coll. D.H. Colless; 23°38'S 134°15'E, Corroboree Rock, 23 March 1978, 1♀; 23°44'S 134°15'E, 39 km E of Alice Springs, 26 September 1978, 1♀—both coll. J. Cardale.

Resembling *P. rieki*, but differing as follows:

Male. *Head* (Figs 16, 17). Gena pale golden pollinose,

but parafacials, parafrontals, and postorbitals silver pollinose. Carina much narrower throughout than epistome, strongly convex in lateral view, protruding by about twice the width of a parafacial, forming a notch above epistome, ground colour golden, slightly pollinose. Facial ridges setulose for only a short distance above vibrissae. Vibrissae set a little above level of epistome margin, about as long as arista, incurved. Frons relatively narrow (Table 3), narrowest in front of ocelli; no fronto-orbitals, but dorsal 2–3 interfrontals reclinate. Gular swelling prominent. *Thorax*. Propleuron bare, apparently weakly sclerotised. Hairs on anterior lappet of posterior spiracle 3–6 in number, very inconspicuous. Setulae beneath posterior margin of scutellum sparse, but extending medially well past bases of second marginal bristles (as usual in Ameniinae). Lower calypter dark on protruding portion, posterior margin rounded. *Legs*. Fore tibia with 0 or 1 *p*, 1 *pv* seta. Mid tibia with usual 1 strong submedian *a* seta, occasionally (1 out of 6 specimens) with 2. Postero-dorsal strip of hind coxa bare. *Abdomen*. T1+2 dark. T3 metallic green with (viewed from behind) median dark vitta and apical dark band, laterally with conspicuous silvery frosting. T4 metallic green, in some lights broadly cupreous medially and darkened apically, sometimes with a trace of pale frosting laterally. T5 more or less similar to T4. *Genitalia* as in Fig. 13; surstyle relatively broad and almost as long as cerci.

Female. Resembling the male in most attributes, but frons narrowest across ocelli, with 2 strong fronto-orbitals.

Distribution (Fig. 26, p. 108). Known only from the vicinity of Alice Springs, Northern Territory, in very arid habitats.

Paraplatytropesa tropicalis n.sp.

Holotype: male; 17°12'S 144°33'E, 6 km S of Chillagoe, Queensland, 27 November 1981, D.H. Colless (malaise trap). ANIC No. 6149.

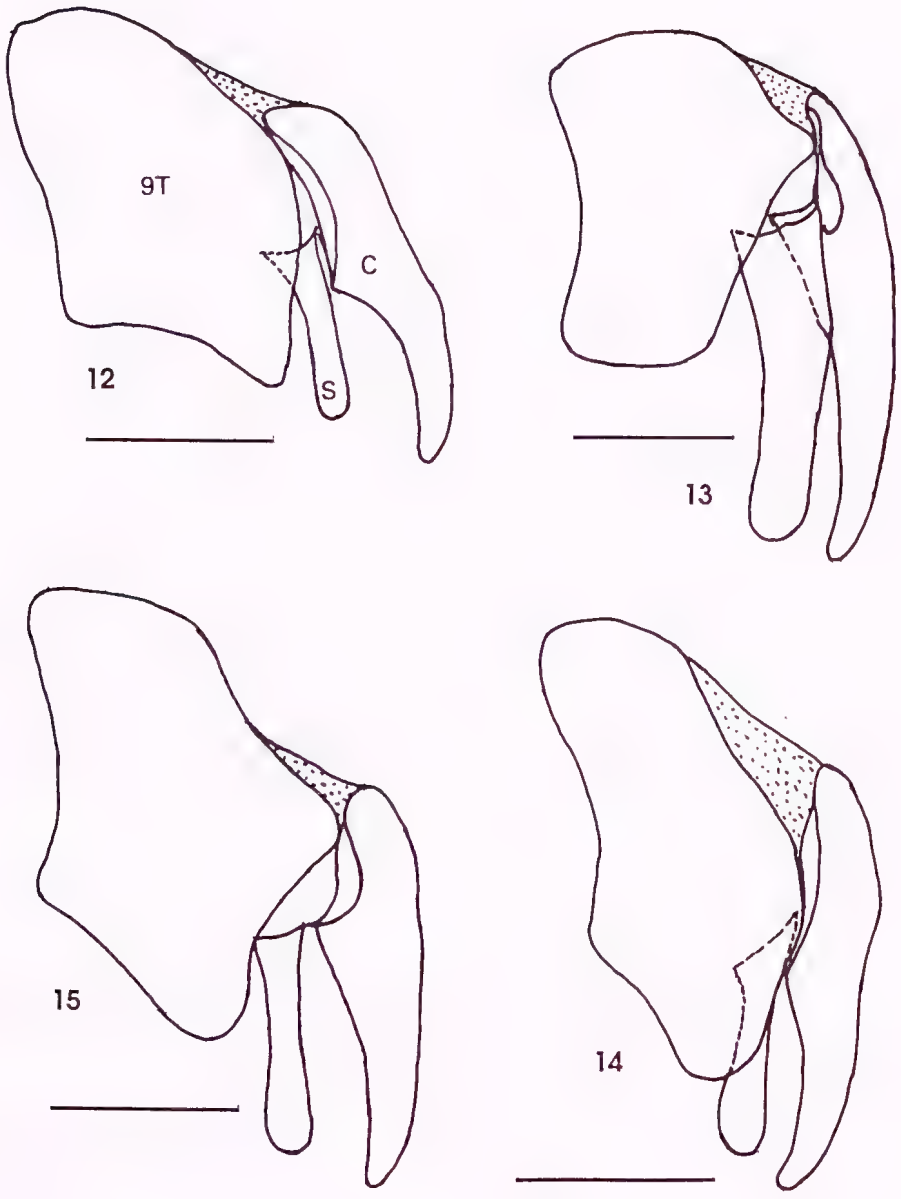
Other specimens examined. QUEENSLAND: 1♂, 1♀, as for holotype; Lakeland Downs Station, SW of Cooktown, 11 September 1969, R.J. Huppatz, 1♀; Helenvale Station, S of Cooktown, 16 September 1969, R.J. Huppatz, 1♀; 13°41'S 143°08'E, Peach Creek, 15 September 1992, P. Zborowski & L. Miller, 1♀ (AM). WESTERN AUSTRALIA: 8 km WSW of Martins Well, West Kimberley, 29 April 1977, D.H. Colless, 1♂; 14°49'S 125°50'E Mining Camp, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J. Cardale, 21♂♂, 13♀♀; 14°35'S 125°45'E, Lone Dingo, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J. Cardale, 19♂♂, 10♀♀.

Very similar to *P. rieki*; relevant attributes as follows:

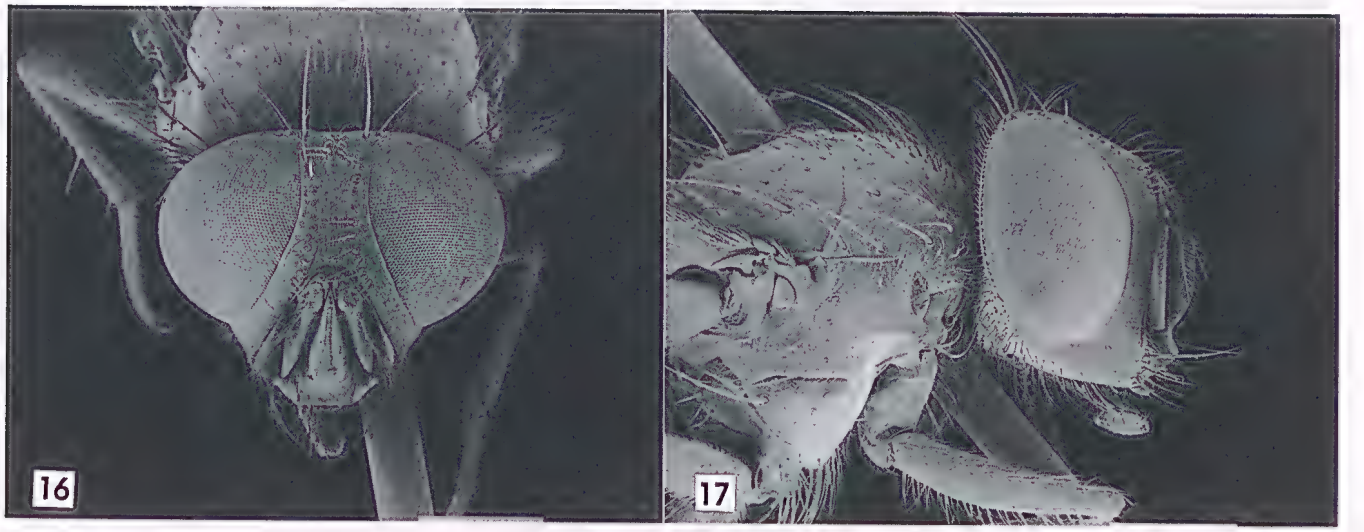
Male. *Head* (Figs 18, 19) . Carina pale brown in ground colour, silver pollinose, confluent with epistome, scarcely protruding past antenna in lateral view. Facial ridge with tiny setulae on some 50-70% of length above vibrissa. Vibrissae set about level with epistome margin, about as long as arista, inclinate but at most slightly decussate. Frons relatively broad (Table 3), with 2 (occasionally 3) strong proclinate fronto-orbitals and 1 (dorsal) exclinate or reclinate. Genae, parafacials, parafrontals, and postorbitals silvery pollinose. Gular region not as strongly swollen as in *rieki*. *Thorax*. Propleuron with profuse setulae. Setulae beneath posterior margin of scutellum sparse, not extending medially past bases of second marginal bristles (as in *rieki*).

Table 3. Selected ratios (ranges and means) for species of *Paraplatytropesa* (numbers of specimens in brackets). Species codes as in Fig. 28. An3l = length of antennal segment 3.

Species			Frw/Hdw	Frw/Frl	Gnw/Hdw	An3l/Hdw
Pa. rie	♂	(4)	0.3–0.4, 0.35	1.5–1.7, 1.52	0.2–0.3, 0.24	0.4–0.5, 0.46
Pa. par	♂	(6)	0.2–0.2, 0.20	0.6–0.8, 0.68	0.2–0.3, 0.23	0.3–0.4, 0.38
Pa. tro	♂	(9)	0.3–0.4, 0.33	1.3–1.6, 1.48	0.2–0.3, 0.23	0.4–0.5, 0.44
Pa. gra	♂	(3)	0.3–0.4, 0.33	1.1–1.2, 1.11	0.1–0.2, 0.16	0.2–0.3, 0.26
Pa. rie	♀	(2)	0.3–0.4, 0.36	1.5–1.5, 1.50	0.2–0.2, 0.23	0.3–0.3, 0.31
Pa. par	♀	(3)	0.2–0.3, 0.27	0.9–1.0, 0.97	0.2–0.3, 0.22	0.2–0.3, 0.28
Pa. tro	♀	(9)	0.3–0.4, 0.34	1.2–1.6, 1.44	0.2–0.3, 0.23	0.3–0.3, 0.29
Pa. gra	♀	(1)	0.32	1.00	0.16	0.26



Figures 12–15. Male genitalia, lateral view. **12**—*Paraplatytropesa rieki*. **13**—*Paraplatytropesa parvifrons*. **14**—*Paraplatytropesa tropicalis*. **15**—*Paraplatytropesa argentea*. Scale bar 0.2 mm; 9T—ninth tergite; c—cercus; s—surstyle.



Figures 16, 17. *Paraplatytropesa parvifrons*, male, facial view (16); lateral view (17). Scale bar 1.0 mm.

Lower calypter pale, posterior angle rounded. Lappet hairs of posterior spiracle numerous in some specimens, but not detected in many others (including holotype). *Legs*. Fore tibia without *p* seta. Postero-dorsal strip of hind coxa with several setulae in about 50% of specimens. *Abdomen*. Tergites metallic green, usually with at least a trace of apical darkening; T1+2 sometimes dark or purplish in some lights, very occasionally with a trace of pale frosting laterally. *Genitalia* as in Fig. 14; surstyles slightly clubbed apically, a little shorter than cerci.

Female. Generally similar to male, but facial ridges setulose over only 20-30% of their length.

Distribution (Fig. 26, p. 108). North Queensland and the Kimberleys; presumably also occurring in intervening areas.

Paraplatytropesa grandicornis n.sp.

Holotype: male; 14°49'S 125°50'E, Mining Camp, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J. Cardale, ex ethanol. ANIC No. 6152.

Other specimens examined. WESTERN AUSTRALIA: 1♂, 2♀♀, as for holotype; 14°35'S 125°45'E, Lone Dingo, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J. Cardale, 1♂.

Generally resembling *P. rieki*, with significant attributes as follows:

Male. *Head* (Figs 20, 21). Carina short, narrow, not confluent with epistome, not protruding past antennal segment 3 in lateral view, dark brown with light silvery pollinosity. Facial ridge with setulae only close to vibrissa. Frons relatively broad as compared with head width, but rather short (Table 3), with 2 strong proclinate fronto-orbitals and 1 reclinate. Antennal segment 3 short, only as long as that of female. Vibrissae set a little above level of epistome margin, conspicuously long and strong, incurved, decussate. Genae, parafacials, parafrontals, and postorbits with silver pollen; gena conspicuously short, truncate (Table 3). *Thorax*. Propleuron with several setulae. Scutellar setulae as for *P. tropicalis*. Lower calypter with exposed portion dark. Lappet hairs of posterior spiracle 1–2 in number, inconspicuous. *Legs*. Fore tibia without *p* seta. Mid tibia with 2–3 strong *a* setae. Postero-dorsal strip of hind coxa setulose. *Wing*. Setulae on basal node of R_{3+4} extending half or more the distance to r-m (in other species, largely confined to the swollen base of the vein). *Abdomen*. T1+2 dark purplish; T3 metallic blue with median dark vitta and apical dark band, and conspicuous, pale silvery lateral patches (in posterior view) extending almost to midline; T4 similar to T3, but pale patches less conspicuous or absent; T5 metallic purplish. S3 with only 4–6 long hairs, S4 without any. *Genitalia* practically identical with those of *P. tropicalis*.

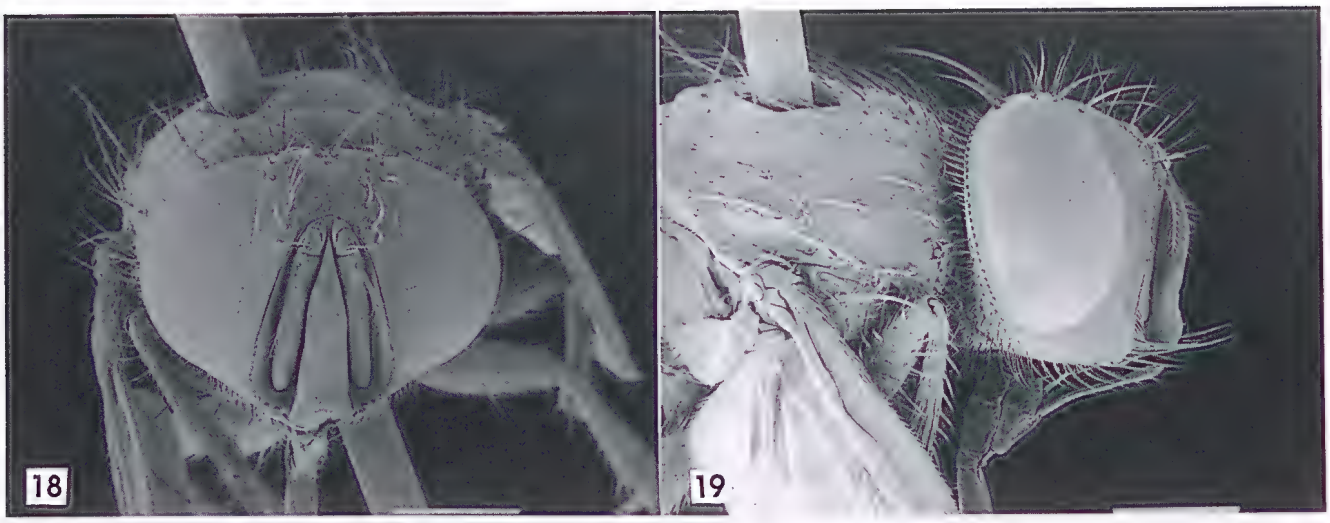
Female. Generally similar to male.

Distribution (Fig. 26, p. 108). Known only from the Kimberleys, Western Australia.

Paraplatytropesa argentea n.sp.

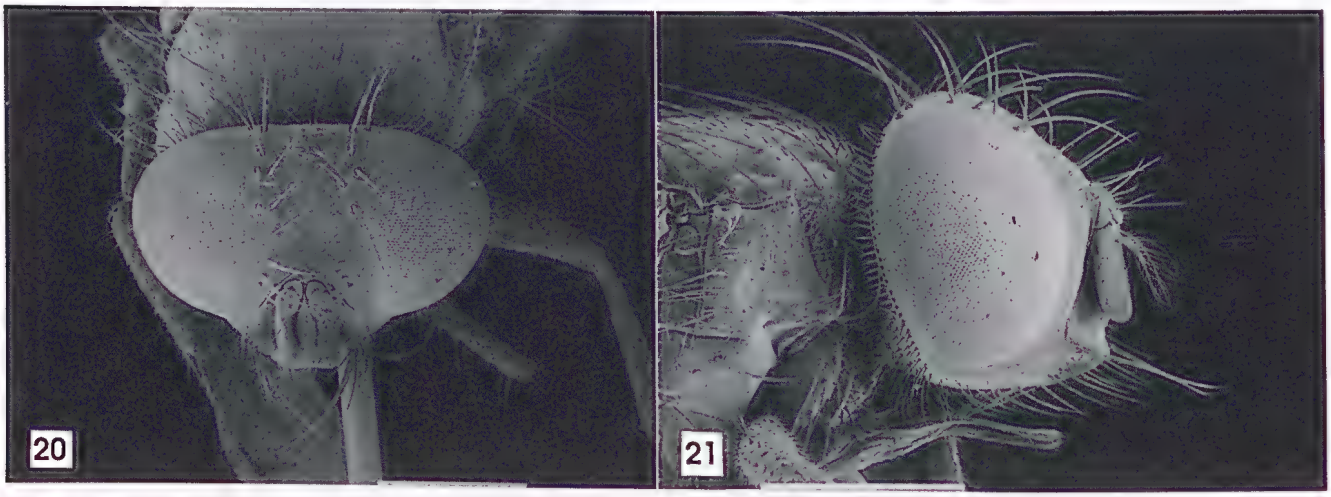
Holotype: male; 12°44'S 143°14'E, 3 km ENE of Mt Tozer, Queensland, 28 June–4 July 1986, D.H. Colless. ANIC No. 6148. The type locality is in the Iron Range area of Cape York Peninsula.

Other specimens examined QUEENSLAND: Banks Island, Torres Strait, 3 June 1969, Neboiss, 1♂ (VM); 12°43'S 143°18'E, 11 km ENE of Mt Tozer, 11–16 July 1986, 1♂; Middle Claudie River, Iron Range, 29 September 1974, G. Daniels, 1♀ (AM); 15°47'S 145°14'E Shiptons Flat, 18 May 1981, 1♂, 1♀; 15°03'S 145°09'E, 3 km N of Mt Webb, 2 October 1980, 1♂; Ellis Beach, N of Cairns, 12 May 1967, 6♀♀. Collected by D.H. Colless unless specified otherwise.

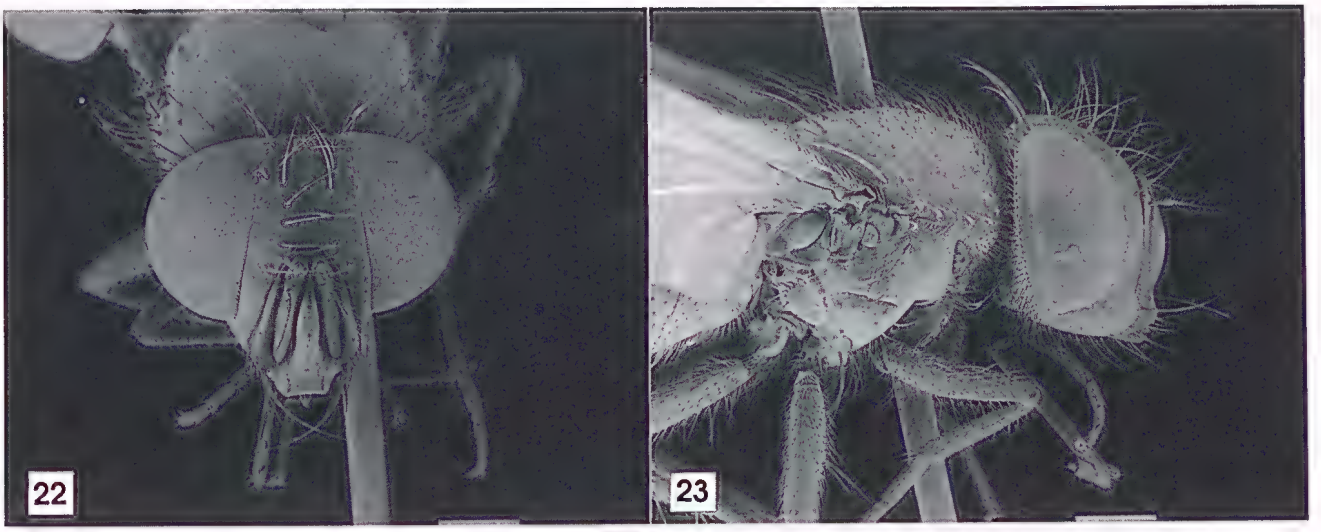


Figures 18, 19. *Paraplatytropesa tropicalis*, male, facial view (18); lateral view (19). Scale bar 1.0 mm.

Male. *Head* (Figs 22, 23) with cerebrale, vertex and a variable amount of parafrontals pale golden pollinose, this merging into silver pollinosity on lateral and ventral portions of parafrontals and most of parafacials, contrasting strongly with deeper golden pollinosity on lower parafacials, genae and postbuccae; postorbits silver pollinose; occiput metallic blue (but with pale pollinosity in some lights). Interfrons rather pale reddish brown. Palps pale brown. Carina and epistoma pale brown with thin pale pollen. Antennal segments 1 and 2 brown, segment 3 pale brown in vicinity of arista, merging into dark brown on the remainder. Parafrontals with sparse dark setulae, few if any along internal margins; interfrons with several dark setulae, none at margins; postbuccal hairs pale golden, those of occiput, parafrontals and genae brown to black. Genal hairs very sparse. Inner eye margins in frontal view only slightly divergent, in some specimens slightly convex below antenna bases. Carina in lateral view protruding, evenly curved, with notch at junction with epistoma; in facial view rounded, not at all flattened anteriorly, tapering from epistoma towards lunula, or somewhat "pinched" on ventral third. In lateral view gular region distinctly swollen, but less conspicuous than in other *Paraplatytropesa* spp. Inner vertical bristles strong, decussate; outer verticals as large as inner; ocellars strongly developed; parafrontal with 2 strong proclinate fronto-orbitals and exclinate prevertical. Vibrissae set distinctly above level of epistoma, decussate and slightly upcurved. Facial ridges with setulae over about the ventral two thirds. *Thorax*. Scutum metallic green with vague cupreous mottling around hair-bases, but in glancing light thinly silver-pollinose over all presutural area, with smaller prealar and postalar patches. Pleura with conspicuous silver spots on anepisternite and sternopleuron. Propleuron haired. *Wing*. Costa without setulae on ventral surface apical to Sc. Membrane slightly infuscated basally and anterior to R_2, and in some specimens along branches of M and crossveins. Lower calypter mainly pale, darkened on posterior and internal margins. M-bend index 1.0–1.5. *Legs* black, with greenish and violaceous reflections on femora. Hind coxa bare on posterodorsal strip. Fore tibia with 1 *p* bristle and 1 *pd* (rarely) or none; *ad* bristles strongly developed. Mid femur with usual anterior group of very strong bristles; mid tibia with 1 strong *ad*, 1 *v*, 2 *p*, and 0-1 *pd*. *Abdomen*. T1+2 dark violet; T3 metallic blue-green, with silvery lateral spots,



Figures 20, 21. *Paraplatytropesa grandicornis*, male, facial view (20); lateral view (21). Scale bar 1.0 mm.



Figures 22, 23. *Paraplatytropesa argentea*, male, facial view (22); lateral view (23). Scale bar 1.0 mm.

extending to midline in glancing light; T4 blue-green with trace of lateral silver frosting in some lights; T5 with conspicuous pair of lateral silver spots. T3 with usual pair of strong median marginal bristles. Sternites dark, with spiny bristles only (no long fine hairs): S2 with 2–3, S3 with 4–6, S4 with 4–6. *Genitalia* rather like those of *Stilbomyella crosskeyi*, but surstyles distinctly swollen apically (Fig. 15).

Female. As for the male, except that parafrontals, parafacials and genae all uniformly golden pollinose and antennal segment 3 uniformly pale brown.

Distribution (Fig. 26, p. 108). North Queensland (Torres Strait, Iron Range, Cooktown, Cairns).

Notes. This species is rather intermediate between *Platytropesa* and *Paraplatytropesa*, and grounds could be found for placing it in the former. Crosskey in fact suggested this on the label of two specimens that he saw but did not describe. Nonetheless, numerical studies support the course that I have adopted here (see Part 3, below).

Genus ***Amenia*** Robineau-Desvoidy

Formosiomima Enderlein, 1936: 444. Type species: *Formosiomima imitatrix* Enderlein, 1936: 444, (= *Amenia nigromaculata* Malloch, 1929), by original designation.

Despite the considerable differences in ornamentation between Malloch's *nigromaculata* and other species of *Amenia*, the structural differences are not great. I am therefore reluctant to follow Crosskey in accepting the generic status proposed by Enderlein (see below) and therefore place his *Formosiomima* as a junior synonym.

Despite much further collecting, *Amenia* has been found (as reported by Crosskey, 1965) only in Australia, especially Queensland and New South Wales; it is present in the Torres Strait islands, but absent from Tasmania. It is sharply separated from other genera by the characters given in the key. See also the note on setulae of the suprasquamal ridge under *Paramenia* (below).

In descriptions of species, I have confined myself to salient, diagnostic features, rather than repeat the detail provided by Crosskey (1965).

Key to species of *Amenia*

1 Abdominal T3, T4, and T5 largely pale grey pollinose with conspicuous pattern of large black spots on their posterior margins (3 on T3, 5 on T4, 1 on T5), the marginal setae standing in groups on the spots. Mesonotum with pair of conspicuous submedian prescutellar pale spots ..... *A. nigromaculata* Malloch

—— Without such pattern on abdomen and thorax 2

2 Scutellum with 3 pairs of marginal bristles 3

—— Scutellum with 4–6 pairs of marginal bristles 6

3 Postorbits silvery white. Hair of genae and postbuccae brownish black. Male frons narrow, but interfrontal strip distinct to ocelli. General colour emerald or cupreous green ..... *A. chrysame* (Walker)

—— Postorbits pale yellow or orange. Hair of genae and postbuccae golden yellow. Male with very narrow frons, parafrontals more or less contiguous. General colour dark blue-green to bluish violet (*leonina* group) 4

4 Abdominal T3 almost always lacking submedian submarginal bristles (very rarely with a weakly developed pair); setulae on central third of T3 appressed (angle less than 45° to surface). Male with head only a little broader than distance between posterior dorsocentral bristles (ratio about 1.2 or less); parafrontal setulae usually relatively short and straight; postorbital strip usually not obliterated, pollinose to or almost to innermost postorbital setae ..... *A. leonina* (Fabricius)

—— Abdominal T3 with at least one submedian marginal bristle, almost always with 2 or more; setulae on central third of T3 relatively erect (angle of 45° or more to surface; Fig. 25). Male with head distinctly broader than distance between posterior dorsocentral bristles (ratio 1.1 or more, except in specimens from New England); parafrontal setulae usually relatively long and at least a few with sharply bent tips (*albomaculata* forms) 5

5 Male with postorbital strip usually more or less obliterated, shiny, anterior to innermost 10 or so postorbital setae ..... *A. albomaculata* (Macquart), typical form

—— Male with postorbital strip well developed, not at all reduced, pollinose to outer vertical seta ..... *A. albomaculata*, New England form

6 Upper occiput non-pollinose, black and semi-shining. Hair of occiput and postbuccae dark brown or black. Wing with bend of vein M much further from margin than from *m-cu*. Thorax black or dark violet with (inter alia) a pair of conspicuous silvery dorsocentral spots at anterior margin. Abdominal T4 with a pair of small white lateral spots ..... *A. longicornis* (Malloch)

—— Upper occiput yellow pollinose over yellow or orange ground colour. Hair of occiput and postbuccae golden yellow. Bend of vein M at most a little further from margin than from *m-cu*. Thorax otherwise, anterior margin without submedian pale spots or with a pair of intraalars and a diffuse median pale area over dorsocentral and acrostichal areas. Abdominal T4 without lateral pale spots 7

7 General colour bright green, sometimes cupreous or bluish green. Scutellum usually with 4 pairs of marginal bristles. Abdominal T4 and T5 without submedian pale spots. Bend of vein M usually about as distant from margin as from *m-cu*. Male with eyes widely separated (*imperialis* group) 8

—— General colour purplish black. Scutellum with 5 or 6 pairs of marginal bristles. Abdominal T3 and T4 each with a submedian pair of silvery spots. Bend of vein M much closer to margin than to *m-cu*. Male with eyes closely approximated ..... *A. sexpunctata* Malloch

8 Upper calypter more than 50% dark, its posterior margin and associated fine hairs dark (or at least brownish) laterally as far as, and including, the external tuft at junction with lower calypter. Male without median marginal bristles on abdominal T3 and hind tibia with conspicuous *ad* fringe of close-set hairs of more or less uniform length (Fig. 24) ..... *A. crinita* n.sp.

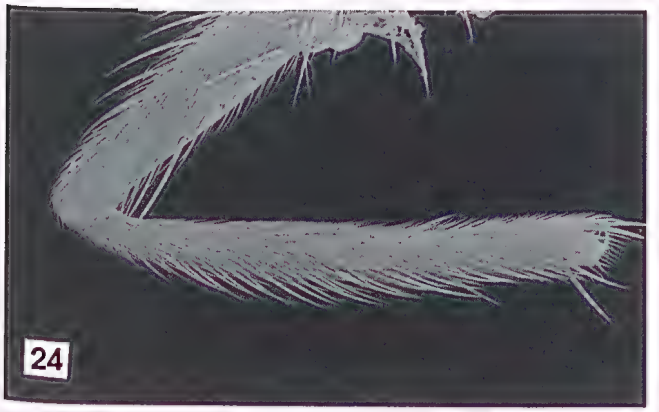
—— Upper calypter dark on little more than the crescent-shaped lobe adjacent to alula and internally along posterior margin, externally (adjacent to lower calypter) the margin and associated fine hairs pure white or (occasionally) slightly golden. Male with pair of strong median marginal bristles on abdominal T3, and hind tibia with rather sparse, irregular *ad* row of several strong bristles mixed with other, much smaller ones 9

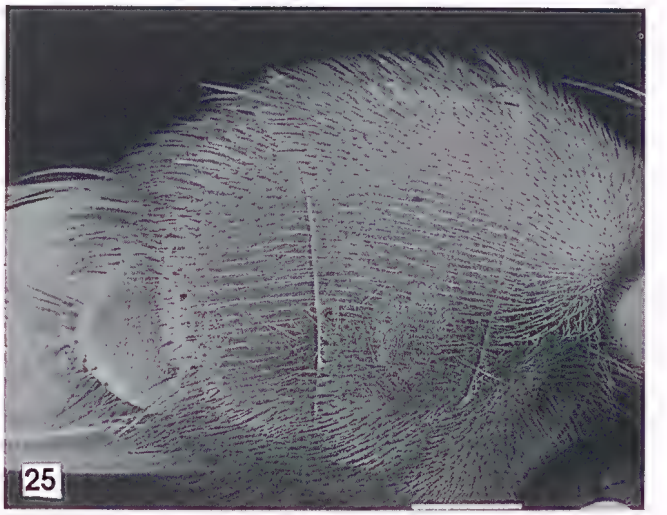
9 Exposed portion of lower calypter (not covered by upper one) pale grey with darkened border. Upper calypter all pale. Female with pair of strong median marginal bristles on abdominal T3; antennal segment ratio about 3. Male with *Frw/Frl* about 0.7; antennal segment ratio about 4; wing with costa only slightly bowed beyond apex of Sc (Northern Territory and Kimberleys) ..... *A. albosquamata* n.sp.

—— Exposed portion of lower calypter all dark brown. Upper calypter usually with at least a little brown colour on posterointernal lobe. Female without median marginal bristles on abdominal T3 (except in southern specimens of *dubitalis*); antennal segment ratio about 2.5. Male with *Frw/Frl* usually less than 0.6; antennal segment ratio usually about 3; wing with costa conspicuously bowed beyond apex of Sc (Eastern Australia) 10

10 Head in direct facial view (lit from above) with conspicuous pale golden pollinosity over genae and parafacials, extending to parafrontals as head is rotated. Male with *Frw/Frl* less than 0.5. Females from south of Brisbane almost always with pair of median marginal bristles on abdominal T3 ..... *A. dubitalis* Malloch

—— Head in direct facial view without conspicuous pollinosity on genae or parafacials, at most a narrow band along eye margins (rotation may reveal some thin pale pollinosity). Male with *Frw/Frl* greater than 0.5. Female without median marginal bristles on abdominal T3 ..... *A. imperialis* R.-Desvoidy





Figures 24, 25. 24—*Amenia crinita*, male, hind tibia. **25**—*Amenia albomaculata*, male, abdomen, lateral view, to show dorsal setulae on T3. Scale bar 1.0 mm.

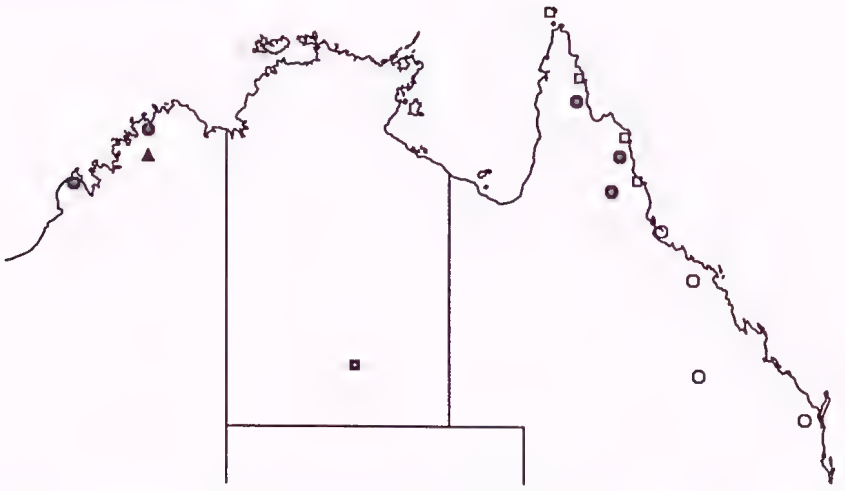


Figure 26. Distributions of *Paraplatytropesa* spp.: filled circles—*tropicalis*; open circles—*rieki*; open squares—*argentea*; filled square—*parvifrons*; filled triangle—*grandicornis*.

Amenia imperialis group

As shown in Part 1, the two "subspecies", *A. imperialis imperialis* and *A. i. dubitalis* are clearly distinguishable, not only by qualitative characters (Crosskey, 1965), but morphometrically as well. Moreover, *dubitalis* is everywhere sympatric with *imperialis*. The case seems, therefore, overwhelming for treating *dubitalis* as a full species, a course foreshadowed by Crosskey (1965) and one that I shall henceforth follow.

The morphometric study also revealed further differentiation within *A. imperialis*, separating off a "Cooktown" and a "Western" form. As shown below, both of these are characterised by additional, qualitative characters. As the "Cooktown" form is everywhere sympatric with typical *imperialis*, and both sexes can be readily identified, I am awarding it, too, full specific status. The case of the "Western" form is more complicated. Its members from the Northern Territory and Kimberleys also possess distinctive qualitative attributes, but there remain several specimens from arid, inland localities in New South Wales and Queensland. These belong morphometrically in the "Western" form, but are otherwise typical *A. imperialis*. The simplest course, and that which I shall follow here, is to recognise the population from the Northern Territory and Kimberleys as a distinct species, treating the other specimens as variants of unknown status (see below: *imperialis*, "arid form").

The principal attribute distinguishing *dubitalis* from the others is the pollinosity of the head in frontal view. For its strict application, the head must be viewed from directly in front, with the light coming at an angle of about 60 degrees and from the direction of the vertex. In the above key, and in the descriptions that follow, these conditions are assumed.

The pair of submedian marginal bristles on abdominal T3 is typically present in males and absent in females. However, they may be present as a rare aberration (female *A. imperialis*), or geographically determined (female *A. dubitalis*), or specifically diagnostic (female *A. albosquamata*). Likewise, in male *A. crinita* lack of the bristles is diagnostic. This suggests variability in some "maleness/femaleness" balance, presumably stemming from some sensitive physiological threshhold. A similar phenomenon occurs in species of *Platytropesa* and *Paraplatytropesa*.

Crosskey (1965) commented on the remarkable uniformity of the male genitalia over most of the Ameniinae. Dissection of a single specimen from each member shows this to hold for the *imperialis* group, with the possible exception of two features mentioned under *A. crinita* and *A. dubitalis*. These are relatively so trivial that I have not pursued them further.

The group as a whole is well characterised by the attributes given in the key. Its members are readily recognised with the naked eye, by the relatively large size, the brilliant green, bluish-green, or cupreous-green colour, without conspicuous pale markings, and the bright golden face.

Amenia imperialis Robineau-Desvoidy **n.stat.**

Amenia imperialis imperialis Crosskey, 1965: 109.

Dr Crosskey has kindly checked his neotype of *A. imperialis* (in the British Museum of Natural History) and my present application of the name is clearly valid. The species is distinguished from others in the group by the attributes given in the key, in particular the non-pollinose parafacials and the colouring of the calypters, and, in the male, the *ad* setae of the hind tibia and the presence of medial marginal bristles on abdominal T3. Also, the M-bend index is 0.9–1.4 (almost always greater than 1.0) and the antennal segment ratio 2.6–3.5 for males and 2.3–3.4 for females. Crosskey's male specimen that lacked bristles on abdominal T3 seems likely to have been the new species, *A. crinita*, described below. On the other hand, I have seen a single female specimen (Kandos NSW, 13–15 May 1981, B.J. Day; AM) that has a male-like pair of submedian marginal bristles on abdominal T3. It is otherwise a perfectly normal specimen of *A. imperialis*.

I have one new rearing record: a male (24 km S of Barraba, NSW, 3 April 1990, P. Colman; AM C.329311) reared from *Galadistes marcescens* (Cox) (Camaenidae).

Distribution. Eastern Australia, from Cape York and Torres Strait Islands to Adelaide, largely on the coast and adjacent ranges, but occasionally taken well inland (Fig. 5; the morphometrically distinct specimens are shown separately.)

Amenia crinita n.sp.

Holotype: male; 15°30'S 145°16'E, 1 km SE of Mt Cook, Queensland, 13 October 1980, D.H. Colless, (at light). ANIC 6155.

Other specimens examined. QUEENSLAND: Lockerbie, Cape York, 2 April 1964, I.F.B. Common & M.S. Upton, 1♀; Bamaga, Cape York, 4 April 1964, I.F.B. Common & M.S. Upton, 1♀; Middle Claudie River, Iron Range, 13 September 1974, G. Daniels, 1♂ (AM); Iron Range, 2–9 June 1971, E.F. Riek, 1♀; 15°03'S 145°09'E, 3km NE of Mt Webb, 1–3 October 1980, T. Weir, 2♀♀; same data, D.H. Colless, 1♀; same data, 3 October 1980, D.H. Colless, 1♀; 15°04'S 145°07'E, Mt Webb NP, 28 April 1981, D.H. Colless, 3♂♂, 1♀; same data, 29 April 1981, D.H. Colless, 1♂; 15°16'S 144°59'E, 14 km NW Hope Vale Mission, 8 May 1981, D.H. Colless, 1♂; Leo Creek, McIlwraith Range, near Coen, 2–3 November 1969, 1♀ (UQ); Bayview, Cairns, 16°57'S 145°43'E, 6 December 1991, C.J. Burwell, 1♀ (UQ); Kuranda, F.P. Dodd, 1♂ (SAM); Cairns District, A.M. Lea, 1♂ (SAM); Mt Bartle Frere (East Base), 80 ft, 29 April 1955, K.R. Norris, 1♀; Palmerston East, Innisfail District, 25 January 1991, D.K. McAlpine & B. Day, 1♂, 1♀ (AM).

This is the "*imperialis* Cooktown form" of Part 1, closely resembling *A. imperialis*, but differing as follows:

Male. *Head*: frons relatively short (Table 2, "Cooktown form"); antennal segment ratio 3.1–3.8. Carina slightly, but distinctly, flatter in profile, less protruding, and therefore less clearly separated from epistome. *Wing*: bend of M relatively closer to wing margin, index 0.6–0.9; upper calypter more than 50% dark, the external margin and associated fringe continuing brown or golden-brown to junction with lower member. *Legs*: hind tibia (Fig. 24) with conspicuous *ad* fringe of close-set bristles of more or less uniform length and strength, about as long as the tibia is wide. *Abdomen*: T3 lacking the usual pair of median marginal bristles. T3 with lateral pale patches reduced, sometimes absent. Genital segments lacking the strong, almost spiny bristles present in other members of the group.

Female. Differing from *imperialis* in the M-bend index and calypter colouration; also, lateral pale patches on abdominal T3 usually absent; antennal segment ratio 2.7–3.2.

Notes. The species was first recognised morphometrically in the male sex only (see Part 1, Fig. 7). Additional diagnostic attributes were later discovered, including the colouration of the calypters, which enabled identification of females. The list of specimens examined includes a number identified since the morphometric studies were made.

Distribution (Fig. 3). North Queensland.

Amenia albosquamata n.sp.

Holotype: male; 14°35'S 124°45'E, Lone Dingo, Mitchell Plateau, Western Australia, 9–19 May 1983, I.D. Naumann & J.C. Cardale. ANIC 6156.

Other specimens examined. WESTERN AUSTRALIA: data as for holotype, 3♂♂, 3♀♀; 14°49'S 125°50'E, Mining Camp, Mitchell Plateau, 9–19 May 1983, I.D. Naumann & J.C. Cardale, 4♂♂, 3♀♀; 8 km S of Cape Bertholet, West Kimberley, 19 April 1977, D.H. Colless, 1♀; Lombardina, 28 May–22 July 1990, G.R. Strickland, 4♀♀; NORTHERN TERRITORY: Brocks Creek, March 1933, T.G. Campbell, 1♂, 1♀; Burnside, 28 March 1929, T.G. Campbell, 1♀; Katherine, 7 January 1964, D. Turner, 1♂ (VM); McArthur River, 48 km SSW of Borroloola, 22 April 1976, D.H. Colless, 1♀; 14°19'S 132°25'E, Katherine Gorge NP, 1 January 1993, G. & A. Daniels, 1♂ (UQ).

This species comprises the Western Australian and Northern Territory populations of the "*A. imperialis* Western form" of Part 1.

Male. Closely resembling *A. imperialis*, differing as follows: *Head*: parafacials sometimes weakly pollinose when head rotated from standard position, away from light (see above); face relatively longer and gena relatively narrower (Table 2, "Western form"); antennal segment ratio distinctly high, 3.5–4.4 due to relatively longer segment 3; arista not reaching apex of segment 3. *Wing*: upper calypter all pale; lower calypter grey or pale, with darker margin. M-bend ratio usually less than 1.0. Costa at most slightly bowed beyond apex of Sc.

Female. Differs from *A. imperialis* in the colour of calypters (as in the male), the presence of a pair of submedian marginal bristles on abdominal T3, and the greater antennal segment ratio, 2.8–3.4.

Distribution. Known only from the Kimberleys, Western Australia, and the Northern Territory.

Amenia imperialis, "arid form"

I am using this name for a set of eight males, from arid areas of inland New South Wales and Queensland, that are seemingly intermediate between typical *A. imperialis* and *A. albosquamata*. They cluster with the latter in the ordination described in Part 1, having, for instance, the typically long face and narrow gena and the long antennal segment 3 (ratio 3.2–4.6 for males). However, the calypters resemble those of *imperialis*, as does the M-bend index.

I suspect that this "form" actually belongs to *A. albosquamata*, and that the morphological separation of the latter from *A. imperialis* is slighter than I am here recognising; indeed, the two "species" may represent the extremes of a cline. But without additional material, I am unable to take the matter further.

Specimens examined. NEW SOUTH WALES: Mt Boppy, near Cobar, 25 November 1949, S.J. Paramonov, 5♂♂; 1 mile

NE of Bohena, Pilliga Scrub, 5 April 1951, Key & Chinnick, 1♂. QUEENSLAND: 28 km NNE of Charleville, 18 October 1978, D.H. Colless, 1♂; 17°12'S 144°33'E, 6 km SE of Chillagoe, 27 November 1981, D.H. Colless, 1♂.

Amenia dubitalis Malloch **rev.stat.**

Amenia dubitalis Malloch, 1927: 343.
Amenia imperialis dubitalis Crosskey, 1965: 111.

Differs from *A. imperialis* in the attributes given in the key. The narrow frons of the male is particularly striking and in both sexes the difference in facial pollinosity, while seemingly rather trivial, is conspicuous under the stated conditions of lighting. For both sexes the M-bend index is 0.7–1.2; the antennal segment ratio is 2.2–3.1 for males and 2.4–2.6 for females.

In the one male dissected the surstylus had a subbasal group of 3–4 bristles on the anterior surface, as opposed to a single bristle for other members of the group.

I have one new rearing record: a male (24 km SE of Bonshaw, NSW, 31 March 1990, P.H. Colman; AM) from *Strangesta* sp. (Rhytididae).

Distribution. Eastern Australia, from about Ingham in the north to southeastern Victoria; restricted almost entirely to the coast and adjacent ranges (Fig. 3) A close examination of records shows a marked deficiency from the more inland localities of southeastern Queensland (Fig. 4), as compared with *A. imperialis* (Fig. 6). The area is well-collected and the difference is clearly significant, presumably reflecting some difference in host snails.

Notes. The difference between females from the border area between Queensland and New South Wales and further south, which almost invariably have submedian marginal bristles on abdominal T3, and those from further north, which almost invariably lack them, could well be used to establish two separate subspecies. However, I see no point in taking this step. The change is quite abrupt, at about the latitude of Brisbane: between there and the 25th. parallel, six out of 13 specimens had such bristles, and further north, only one out of 21 (and that very small). Per contra, only two out of 47 specimens from more southern localities (Sydney and Narrabri) lacked such bristles, two had only a single bristle, and two had three bristles.

Amenia chrysame (Walker)

Material now available extends the distribution to far North Queensland and, in the south, to the Flinders Ranges, north of Adelaide (Fig. 10). The morphometric analysis in Part 1 (Fig. 11) revealed a sharp discontinuity in variation at about the 26th parallel, in the vicinity of Bundaberg. Further study shows that males from north Queensland have the postorbital strip less reduced than have those from New South Wales. In the former, the pruinosity can be traced to or almost to the vertex; in the latter it disappears well before the vertex. A slight difference in the shape of the carina, in both sexes, also shows a similar distribution. However, between the New South Wales border and about Bundaberg, the two forms seem to overlap and intermediates are found. Despite this clear evidence of subspeciation, I see no reason to give it formal recognition.

A. chrysame has the submedian marginal bristles on abdominal T3 very strongly developed, both in size and (in males only) in number (usually 4 or 5, but up to 7 have been seen).

Distribution (Fig. 10). Eastern Australia, predominantly on the coast or nearby ranges, from Cape York to the Flinders Ranges, South Australia.

Amenia leonina group

This group comprises the two taxa treated by Crosskey (1965) as subspecies of *A. leonina*: *A. l. leonina* and *A. l. albomaculata*. As discussed in Part 1, the two are to a large extent allopatric, but with some significant occurrences of each within the range of the other. Males are morphometrically distinct on the basis of relative head width, which correlates with the other characters used in the key above, but in southeastern Queensland, in the general vicinity of Brisbane, intermediate specimens occur, suggesting some degree of introgression of genotypes. However, this could be the result of ecological disturbance, and specimens of *A. albomaculata* from Mackay and of *A. leonina* from Sydney, suggest that introgression is not general. For that reason, specific status seems to me most suitable, and I am restoring the taxa on that basis.

Members of the group can be identified by the characters given in the key. They can be recognised with the naked eye by the large size, the metallic blue or greenish-blue body colour, the conspicuous pair of prescutal dorsocentral pale stripes, and the pale lateral spots of abdominal T3 not extending on to the dorsum. The rather similar *A. longicornis* is usually smaller, purplish-black in colour, and the lateral pale spots on T3 clearly extend on to the dorsum. As in the *imperialis* group, the male terminalia show no attributes useful for identifying the group or its individual species.

Crosskey's (1965) detailed descriptions hold fairly well, and I deal below mainly with additional differences that have appeared in the more abundant material now available. The curious geographic distributions displayed in this group are discussed in Part 3 (Zoogeography and Evolution).

Amenia leonina (Fabricius) **n.sens.**

Amenia leonina leonina, Crosskey, 1965: 113.

The characters given in the key serve, together, by weight of evidence, to identify all male specimens seen so far; but every character fails very occasionally. I have three males (from near Cooktown) that have a small, but distinct pair of submedian marginal bristles on abdominal T3; another three have the parafrontal bristles long and with bent apices; another has the postorbits partly obliterated; and, as shown in Part 1, four others have the broad head typical of *A. albomaculata*. Also, the appressed setulae on

the central third or so of abdominal T3, although almost always evident, were in a few specimens not clearly developed. Nonetheless, in every case the characters jointly gave a convincing identification. The rather greenish hue of the thorax and (sometimes) the abdomen is also of some use. Of other attributes listed by Crosskey (1965), I find that the ocellar setae are by no means "weak", but usually just as strong as in *A. albomaculata*.

I have examined the specimens of *A. leonina* from Sydney, listed by Crosskey (1965), and can confirm that they are quite definitely of this species.

Distribution (Fig. 8). Largely coastal, from the Kimberleys east to the Queensland-New South Wales border; replaced in New South Wales by *A. albomaculata*, except for one known occurrence in the vicinity of Sydney; then reappearing in central Victoria and the eastern part of South Australia (including Kangaroo Island). The reason(s) for this peculiar distribution remain obscure.

Notes. One of the specimens from South Australia was reared from a "caenenid" snail (sic; ?camaenid).

Amenia albomaculata (Macquart) **rev.stat.**

Amenia leonina albomaculata, Crosskey, 1965: 115.

There is no difficulty in identifying the species, using the combination of characters given in the key. The submedian bristles on abdominal T3 alone serve for all specimens of *A. albomaculata* seen to date. Of the remaining male attributes, the semi-erect setulae on T3 (Fig. 25) are also reliable, as are the others if the "New England" form (see below) is excluded. Also of some use is the not infrequent reduction or absence of the presutural silvery patch (on the suture, mesad of the presutural bristle), which seems usually present in *leonina*.

I have three enigmatic males from the vicinity of Brisbane that resemble the "New England" form (see below) in having the parafrontal setae as in *leonina* , but the postorbits are intermediate between that form and the typical one. Their status remains unclear.

Geographic forms.

Two geographically circumscribed forms were first noticed during the morphometric analyses, by virtue of their relatively broad frons (Fig. 9, p. 94). Fuller study revealed other distinctive attributes.

(a) "New England" form.

This form is represented by 16 male specimens from the New England area, above 1,000 metres. As shown in Fig. 9, the relative frons width, although distinctive, does not completely separate them from typical specimens. However, all have unmodified, pollinose postorbits (and hence relatively narrow heads; see Fig. 9); 14 have the parafrontal setulae short and straight; and two have the setulae of abdominal T3 somewhat appressed; i.e., in these attributes they resemble *A. leonina* rather than *A. albomaculata*. Only one male from that area (from two taken together in New England NP) clearly belonged to the typical form. There are 13 associated females that presumably belong to this form, but cannot be differentiated from the typical one on female attributes.

It seems probable that we have here a population conditioned by adaptation to a different host that frequents higher altitudes. However, its taxonomic status remains unclear.

(b) "Southern" form

This form comprises six males and 11 females from the western shore of Spencer Gulf, South Australia (mostly from the tip of Eyre Peninsula). Two females from Albany, Western Australia, could be included here also. The males are moderately distinct in having the frons relatively wide (Fig. 9, p. 94), and both sexes have the dorsal thorax rather dull and blue-black, rather than the brighter, metallic blue of the typical form. This colour difference is most clearly seen with the naked eye. Also, two females and two males were unusual in having 1–2 discal bristles on abdominal T3.

Considering the isolation of this form from the typical one (Fig. 8), it is perhaps surprising that so little morphological differentiation has occurred. There is certainly insufficient to consider specific status.

Distribution (Fig. 8). Queensland (mainly in the extreme south), New South Wales, and eastern Victoria; reappearing as the "Southern" form in South Australia, west of Spencer Gulf, and at Albany, Western Australia. Not so markedly confined to the coast and adjacent mountains as *leonina*, and extending well inland in the 3 eastern states.

Amenia longicornis (Malloch)

As shown in Part 1, the species comprises two fairly distinct geographic forms: an eastern one, found around the head of Spencer Gulf and north through the Flinders Ranges to the MacDonnell ranges of the Northern Territory, and a western one in places west of about 135° longitude. Although qualifying as geographic subspecies, I see no point in naming them formally.

Two specimens from the Flinders Ranges were reared from snails of the species *Sinumelon hawkerana* Solem (Camaenidae) (near Jonburgh, South Australia, M. Newton, 27 May 1992)

Amenia sexpunctata Malloch

The currently known range of this species (Fig. 10) extends from the general vicinity of Darwin, through Arnhem Land (including the Cobourg Peninsula) and the McArthur River coast, to Cape York Peninsula (vicinity of Weipa and Iron Range). Crosskey doubted its occurrence in North Queensland, due to Paramonov's (1957) somewhat misleading description of a specimen that had the (eye) "facets very enlarged". This is in fact true of all males of the species, in that facet size gradually increases from the ventral and posterior margins to the forward-looking area near the middle of the frons; the latter facets are about three times as broad as

the former. However, this hardly differs from the general condition in ameniines, in which the increase is about two times—a figure, moreover, that seems to correlate roughly with size. *Amenia sexpunctata* is one of the largest of the ameniines. Its size, plus its very dark colour and the paired pale spots on abdominal T3, T4, and T5 make it easily recognisable with the naked eye.

Amenia nigromaculata Malloch

Formosiomima nigromaculata Crosskey, 1965: 124.

The species has a largely coastal distribution in southwestern Australia, from Exmouth Gulf in the north and eastwards along the Great Australian Bight as far as Yalata in South Australia (Fig. 10). Although overlapping broadly with *A. longicornis*, it occurs alone along the western and southwestern coasts of Western Australia. This is no doubt correlated in some fashion with the biology of the host-snails, which are species of *Bothriembryon* (Orthalicidae): *B. balteolus* Iredale, *B. bulla* Menke and *B. glauerti* Iredale (Ferrar, 1976).

The phylogenetic evidence in Part 3 (Figs 20–22) suggests that *A. nigromaculata* is the sister species of *A. chrysame*. This is consistent with their complementary distributions in areas that differ markedly in rainfall. Separate generic status for the former species would therefore be quite inappropriate, despite its conspicuously different colour pattern. This is not accompanied by any significant structural differences, and is presumably due to a long period of isolation in southwestern Australia in a different host snail (I am indebted to a referee for the information that *A. chrysame* lives largely (?entirely) outside the range of *Bothriembryon*).

Tribe Parameniini

I am including in this tribe the mainly Oriental genus *Catapicephala*, which was added to the subfamily by Kurahashi (1989), but placed in its own, monotypic tribe (he also adds West Irian to the range of *C. splendens*). I do this on good phenetic grounds. Examination of a specimen of each sex of *C. splendens* Macquart and a female of the type species, *C. ingens* (Walker), shows that they closely resemble *Paramenia* spp. in the relatively large size, the rather distinctive coloration, the absence of the facial carina and apical *pv* spine on the hind tibia, and the presence of a posthumeral bristle set in front of or a little externally to the presutural bristle. These attributes are probably all plesiomorphic, and the tribe may well be paraphyletic; but that is a small price to pay for a more balanced classification. (A referee has pointed out that, in any case, *Catapicephalini* Kurahashi, 1989 is a *nomen nudum*).

Genus *Paramenia* Brauer & Bergenstamm

The genus, which is confined to Australia and New Guinea, is very distinct: principally in lacking the facial carina, which is well developed in other genera (differences from the non-Australian *Catapicephala* are given in the key to genera). Unlike other ameniines, the prosternal setae may also be reduced or absent, an attribute that was regarded by Crosskey (1965) as of little or no taxonomic use within *Paramenia*. Per contra, I find that there are always at least 2–3 fine hairs present in *P. semiauriceps* (63 specimens) whereas they are almost always lacking (6/7♂♂, 9/10♀♀) in *Paramenia angustifrons*. I have added this feature to the key below, as well as the difference in relative width of the gena. Crosskey noted the latter feature, but I have used my own system of measurement (see Part 1). I might add that PCA of a set of head dimensions (not shown) clearly separates the two species.

I can add nothing else to Crosskey's detailed descriptions, beyond noting that both species have a small tuft of setulae on the suprasquamal ridge, as in all the large species of *Amenia* (i.e., excluding *chrysame* and *longicornis*).

Key to Australian species of *Paramenia*

1 Males 2

—— Females 3

2 Eyes almost meeting in midline, frons reduced to a very narrow strip no wider than anterior ocellus. Parafrontals pale yellowish grey or silvery grey pollinose. Prosternum usually bare ..... *Paramenia angustifrons* Crosskey

—— Eyes more widely separated, frons about three times as wide as anterior ocellus. Parafrontals bright yellow pollinose. Prosternum with at least a few fine setae ..... *Paramenia semiauriceps* Brauer & Bergenstamm

3 Mid-tibia with at least one weaker, more basal *ad* seta in addition to the submedian one. *Gnw/Hdw* 0.27–0.31, av. 0.30. Prosternum with at least a few fine setae ..... *Paramenia semiauriceps* Brauer & Bergenstamm

—— Mid-tibia with one strong isolated submedian *ad* seta. *Gnw/Hdw* 0.22–0.26, av. 0.25. Prosternum usually bare ..... *Paramenia angustifrons* Crosskey

Paramenia semiauriceps Brauer & Bergenstamm

Crosskey (1965) doubtfully assigned to this species a specimen (from Byfield, Queensland) that lacks the second, more basal *ad* bristle on the mid-tibia. I have studied this specimen and find that it clusters clearly with females of *semiauriceps* in a PCA ordination. Apparently the tibial bristling can vary somewhat.

The female from the AM recorded by Ferrar (1976) as reared from *Meridolum gulosum* (Camaenidae) now stands with a labelling correcting that to *M. middenense* McLauchlan.

The distribution is shown in Fig. 27. The range is there provisionally extended to South Australia on the basis of two specimens in the AM labelled (simply) with the name of the state. There are grounds for regarding such records with suspicion, but the implied extension is not unlikely and I am prepared here to accept it.

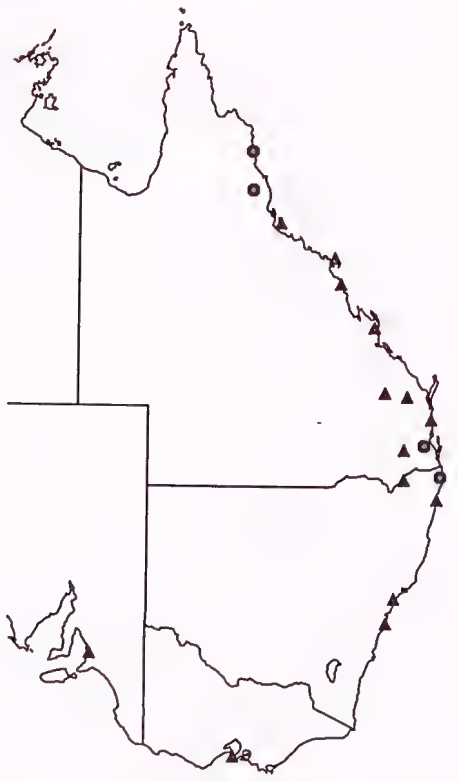


Figure 27. Distributions of *Paramenia* spp.: circles—*angustifrons*; triangles—*semiauriceps*. Records from (simply) "South Australia" are provisional and shown, for want of better, as from Adelaide.

Paramenia angustifrons Crosskey

I have seen two of the the three specimens from Highvale (14 miles NW of Brisbane), Queensland, that Crosskey (1965) thought might represent a new species, largely on the basis of head shape. Using my own system of measurement (which I believe to be more accurate) I find little difference between these specimens and typical *Paramenia angustifrons*, with which they cluster closely in a PCA ordination (not shown).

The range of the species is shown in Fig. 27. It seems restricted to the tropics and subtropics.

PART 3. CLASSIFICATION AND ZOOGEOGRAPHY

I start from the hypothesis that the current classification, as used in Part 2, is reasonable and useful. That is my "positive heuristic" in a Lakatosian "research programme" (Lakatos & Musgrave, 1970). The classification is then compared with the phenetic structure found by numerical studies of a substantial set of characters, in the belief that the degree of such consistency is a measure of the utility of a classification. I also believe that phenetic structure provides a useful hypothesis of phylogenetic structure (Colless, 1970; Saitou & Nei, 1987; Avise, 1994—the last *teste* Wallman & Adams, 1997), which may help illuminate the zoogeography of the group. This is especially true of the Neighbour-Joining algorithm, which, despite its phenetic flavour, was explicitly devised to reveal phylogenetic structure (Saitou & Nei, 1987).

Numerical studies

Phenetic structures were examined using a set of 26 species (listed at Fig. 28) and 54 morphological characters (see Appendix). For the geographically variable *Amenia dubitalis* and *A. chrysame*, the northern and southern forms respectively were employed. The New Guinean *Stilbomyella nigrocostalis* and *S. nitens* were included for comparison with the two Australian species. Also, a female of the Indonesian *Silbomyia mackerrasi* Crosskey was included to fill out that genus, otherwise represented by just four specimens of the two Australian species. For phylogenetic purposes, two related species were also included: *Phumosia surcoufi* (Bezzi) and *Euphumosia papua* (Guérin-Méneville). These were chosen on the criterion of maximum applicability of the characters employed for the study group. The character matrix is shown in Table 5.

Because of variation within species, many entries in the matrix represent the *usual* condition as observed over a representative set of specimens. Likewise, some entries were rather arbitrary, due to my inability to draw sharper boundaries between states. The data proved robust under the test of comparing results using odd-numbered characters only, and then even-numbered characters only, with each other and with results for the whole set. This was done using Manhattan distances from range-coded data, sorted by UPGMA and Neighbour-Joining algorithms. Trees were compared by counting shared components (subtrees). The percentages shared were as follows:

Neighbour-Joining: complete set *vs* even—70, complete *vs* odd—74, even *vs* odd—56.

UPGMA: complete set *vs* even—60, complete *vs* odd—76, even *vs* odd—68.

All genera and species-groups recognised in Part 2 above remained practically intact using both reduced sets of data. Changes consisted mainly in rearrangements within genera.

After some preliminary tests of ordinations, phenetic structure seemed most succinctly displayed by the Minimum Spanning Tree (Fig. 28), in which all genera and species groups recognised in Part 2 are clearly clustered. For *Stilbomyella anomala* and *Paraplatytropesa*

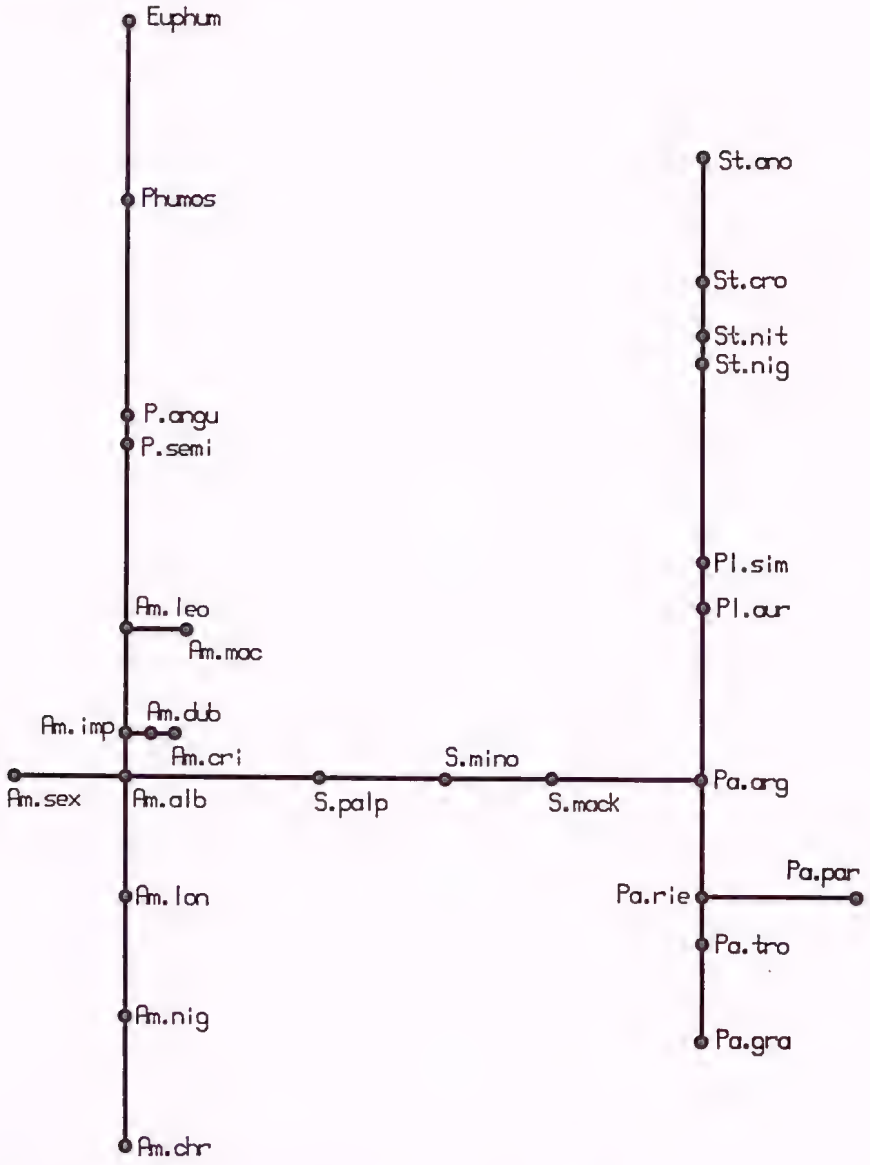


Figure 28. Minimum spanning tree on 26 Ameniini and 2 outgroups; Manhattan distances, to scale. Species codes: Euphum—*Euphumosia papua*; Phumos—*Phumosia surcoufi*; P. angu—*Paramenia angustifrons*; P. semi—*Paramenia semiauriceps*; Am. leo—*Amenia leonina*; Am. mac—*Amenia albomaculata*; Am. imp—*Amenia imperialis*; Am. dub—*Amenia dubitalis*; Am. cri—*Amenia crinita*; Am. sex—*Amenia sexpunctata*; Am. alb—*Amenia albosquamata*; Am. lon—*Amenia longicornis*; Am. nig—*Amenia nigromaculata*; Am. chr—*Amenia chrysame*; S. palp—*Silbomyia palpalis*; S. mino—*Silbomyia minor*; S. mack—*Silbomyia mackerrasi*; Pa. arg—*Paraplatytropesa argentea*; Pa. rie—*Paraplatytropesa rieki*; Pa. par—*Paraplatytropesa parvifrons*; Pa. tro—*Paraplatytropesa tropicalis*; Pa. gra—*Paraplatytropesa grandicornis*; Pl. aur—*Platytropesa auriceps*; Pl. sim—*Platytropesa simulans*; St. nig—*Stilbomyella gloriosa*; St. nit—*Stilbomyella nitens*; St. cro—*Stilbomyella crosskeyi*; St. ano—*Stilbomyella anomala*.

argentea this agreement is gratuitous, since their generic positions were finally decided on phenetic grounds. However, all other detail was derived from the the current classification plus my recent additions.

The phenograms yield a similar result. I computed a set of 10 (Nearest Neighbour, Furthest Neighbour, UPGMA, WPGMA, Lance & Williams Flexible [3], Incremental Sums of Squares [3]) with varying intensities of clustering. Then, following a criterion mentioned in Colless (1994: 521), I chose the one with the least variability in internode length: Furthest Neighbour (Coefficient of Variation = 0.696). This is shown as Fig. 29, p. 115. That for UPGMA was a close runner-up (C. of V. = 0.716), differing in only 1 component (*A. sexpunctata* shifts position). Again, the classification in Part 2 is well supported. [The criterion just mentioned—C. of V. of internode length—is a measure of what has been called "stemminess" by Fiala & Sokal (1985), and correlates highly with their coefficient].

The Neighbour-Joining algorithm yielded the dendrogram shown in Fig. 30. Rooted by the two outgroups, *Phumosia surcoufi* and *E. papua*, it closely resembles the others; ignoring the outgroups, 75% of its components are shared

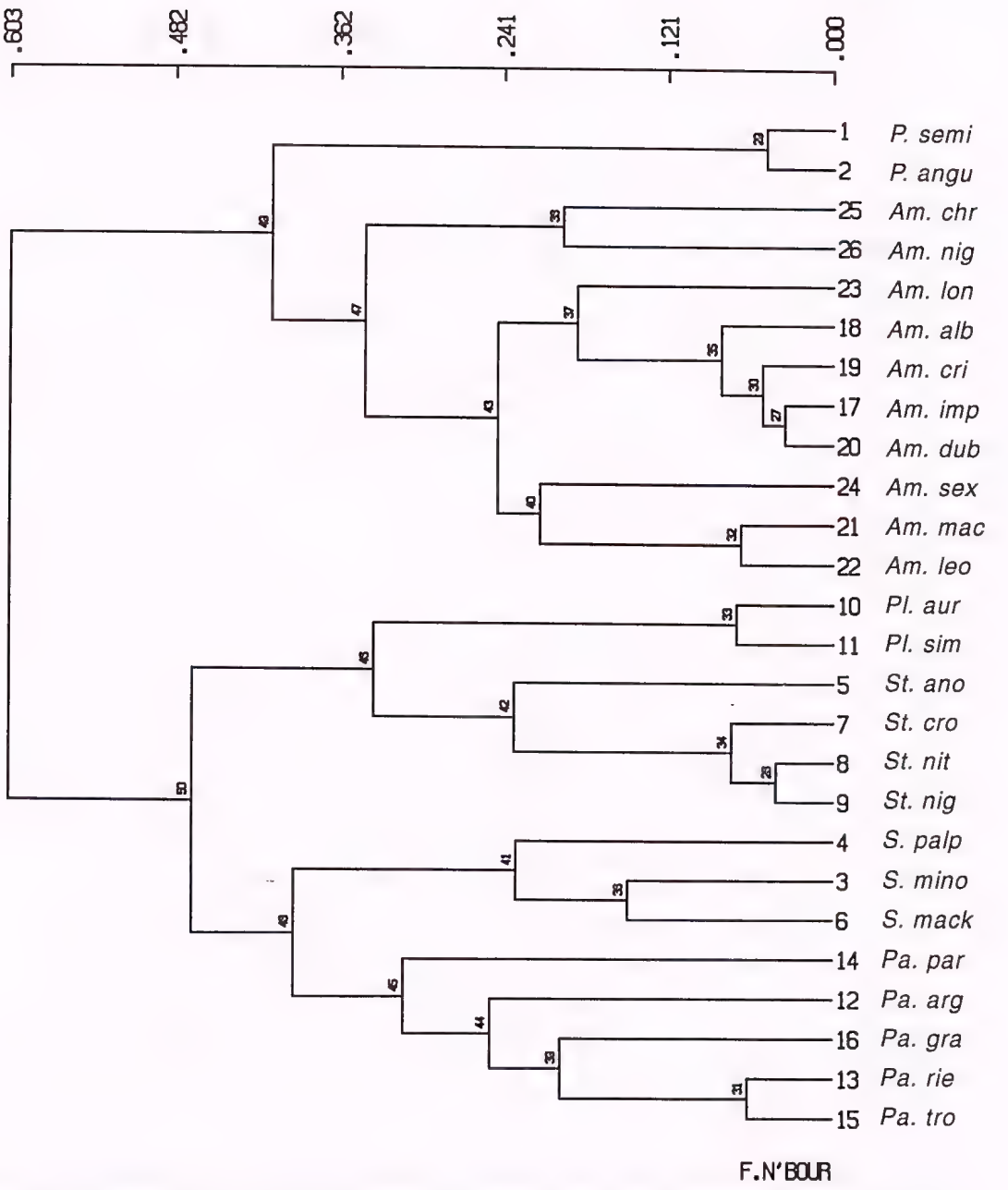


Figure 29. Phenogram for 26 Ameniini; Manhattan distances and furthest neighbour. Codes as in Fig. 18.

with the Furthest Neighbour phenogram. The only major difference lies in the placement of the "primitive" *Paramenia* with *Amenia* in Fig. 29, p. 115, which is explicable as a result of symplesiomorphy. There are grounds, therefore, for accepting the broad details of Fig. 30 as faithfully reflecting the phylogeny of the subfamily.

I conclude that the classification used in Part 2 is in fact a reasonable one: especially as regards the generic placement of *A. nigromaculata, St. anomala*, and *Paraplatytropesa argentea*. The tribal status of *Paramenia* also seems reasonable. However, it is clear that *Amenia* could itself constitute a tribe of its own, with *Silbomyia, Platytropesa, Stilbomyella*, and *Paraplatytropesa* forming another tribe. Indeed, the phenogram (Fig. 29, p. 115) would argue strongly for such a course. I have, nonetheless, refrained from adopting this formally, because it does smack of classificatory overkill, and because the new taxon names would have to be defined by complex, polythetic definitions. They would, in my view, serve little if any purpose.

Zoogeography and evolution

It seems very likely that Ameniinae arrived in Australia as immigrants from islands to the north (Colless & McAlpine, 1991), either at some time when the continent was connected to New Guinea, and/or was only narrowly separated from Timor. Crosskey (1965) suggested that *Silbomyia* entered via the Timor route because the genus is absent from New Guinea and the Moluccas. This was made even more likely by the subsequent discovery of *S.*

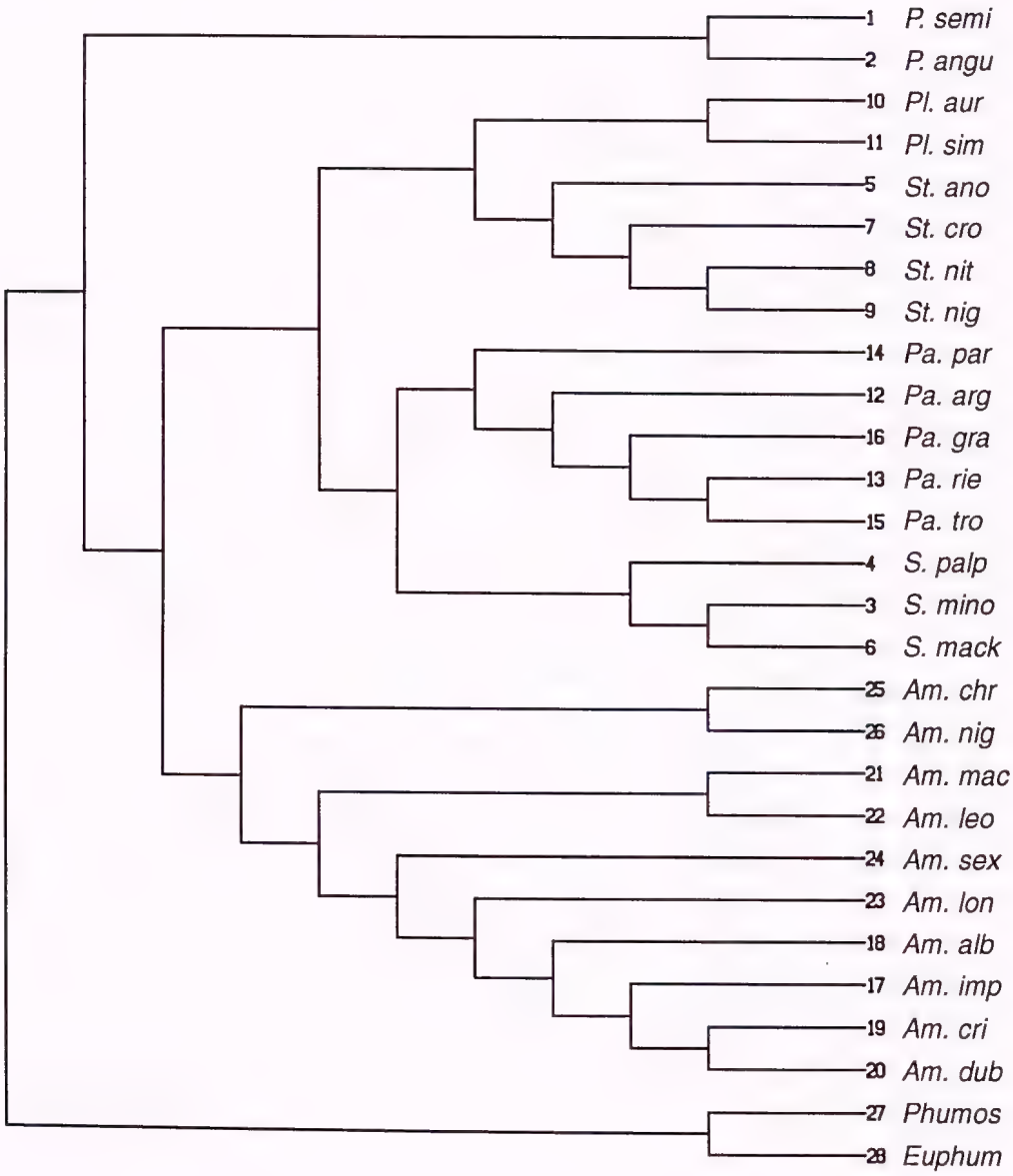


Figure 30. Dendrogram for 26 Ameniini and 2 outgroups; Manhattan distances and neighbour-joining. Codes as in Fig. 18.

palpalis in northwestern Australia. Indeed, the very wide distribution of *Silbomyia*, through India, China, and Southeast Asia makes it a fair candidate to represent the parental stock of the subfamily in Australia. On the other hand, *Platytropesa, Stilbomyella,* and *Paramenia*, which are all distributed in Australia, New Guinea and (for the first two) the Moluccas, may well have arrived here from the north. Alternatively, they may have actually originated in Australia and made their way back to New Guinea and islands to the west.

Little of the foregoing is supported by phylogenetic evidence, and it takes no account of the somewhat enigmatic *Catapicephala* (see above). That genus, widely distributed in the Oriental Region (Malaysia, Indonesia, and Taiwan; Senior White *et al.*, 1940), shows distinct resemblances to *Paramenia*, but the attributes concerned are very probably plesiomorphic and do not necessarily argue for close phylogenetic relationship. Nonetheless, these two are clearly "primitive" genera, and the position of *Paramenia* in Fig. 30 suggests that it, rather than *Silbomyia*, represents the ancestral stock. Its distribution overlaps only slightly with that of *Catapicephala* (*C. ingens*, in western New Guinea), and the Australian ameniines might well have originated in a vicariance event that yielded *Catapicephala* in the Moluccas and *Paramenia* in New Guinea. The latter then entered Australia via Cape York (statements concerning the "evolution", "migration", etc., of a genus are, of course, to be construed as referring to some ancestral species that we would place in that genus). There is no evidence whether *Stilbomyella* and/or *Platytropesa* differentiated in New Guinea and migrated into Australia or vice versa; but it does seem plausible that *Silbomyia* evolved on the mainland, along with its sister-group, *Paraplatytropesa*. This would imply that

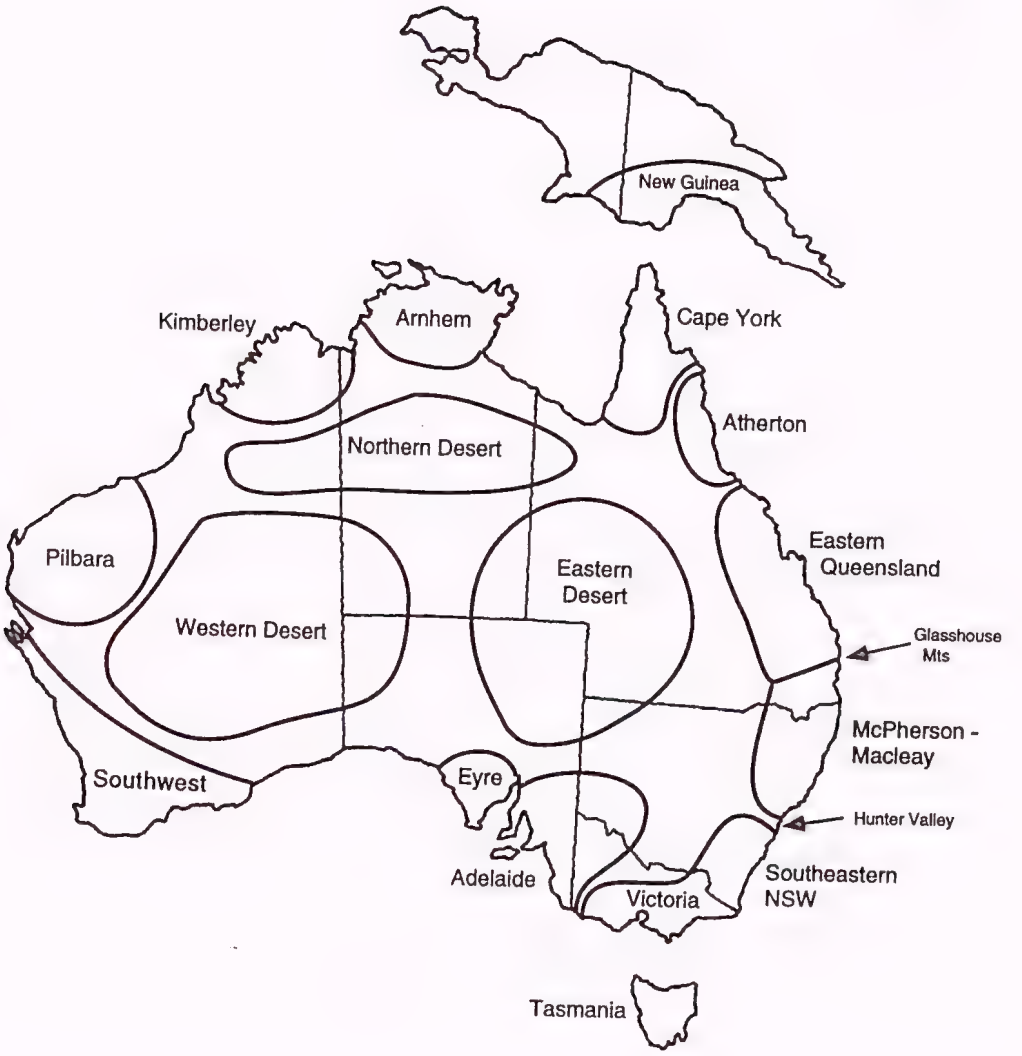


Figure 31. Map of Australia and New Guinea showing "provinces" used in this study (from Crisp *et al.*, 1995).

Silbomyia then back-migrated into Asia via Timor. Alternatively (and more parsimoniously), *Silbomyia* may have originated in Asia and entered Australia independently from the northwest, as in Crosskey's scenario. I see little hope of a decision on these matters.

The foregoing speculations aside, there remains a body of reasonable evidence supporting the holophyly of all recognised genera, as attested by all methods of analysis. Of relationships within genera, the *imperialis* and *leonina* species groups, within *Amenia*, are credibly holophyletic—scarcely surprising, their members are separable only with careful examination! The grouping of *A. longicornis, A. nigromaculata,* and *A. chrysame* also seems credible. As mentioned in Part 2, *A. nigromaculata* is credibly the sister species of *A. chrysame*, on grounds of morphology and distribution; likewise, *A. longicornis* is credibly an earlier migrant to southwestern Australia, and sister species to *A. nigromaculata* + *chrysame*. *Amenia albosquamata* appears to be the sister species to the rest of the *imperialis* group—presumably a western vicariant, but other relationships within the group seem hopelessly obscure. Of others, *A. leonina* is clearly sister to *A. albomaculata*, presumably as north-south vicariants; but the picture is clouded by the (?)relict populations found in South and Western Australia, which suggest a very complex, but currently unguessable history. Finally, in *Stilbomyella, S. anomala* is credibly sister to the rest of the genus, as is *S. crosskeyi* to one or both of the New Guinean vicariants, *S. gloriosa* and *S. nitens*. Of *Amenia*, one can only presume that it evolved from a very early migrant from the north, rapidly differentiating to colonise the whole continent. It is a fair speculation that such a process would have been greatly assisted, even accelerated, by access to an untouched field of host snails.

Turning to distributions, which are now tolerably well known, all ameniines show distinctive ranges that no doubt reflect the history of their dispersal and vicariant evolution. However, we face at the outset the problem that probably all are parasites of land snails and that their distributions will be to an unknown degree influenced by those of their hosts; and no doubt there will have been some coevolution and and/or opportunistic switching of hosts in allopatric populations. But we know so little at present of the actual hosts of ameniine species that, even if the snail phylogeny were credibly established, it would provide little input to zoogeographic studies.

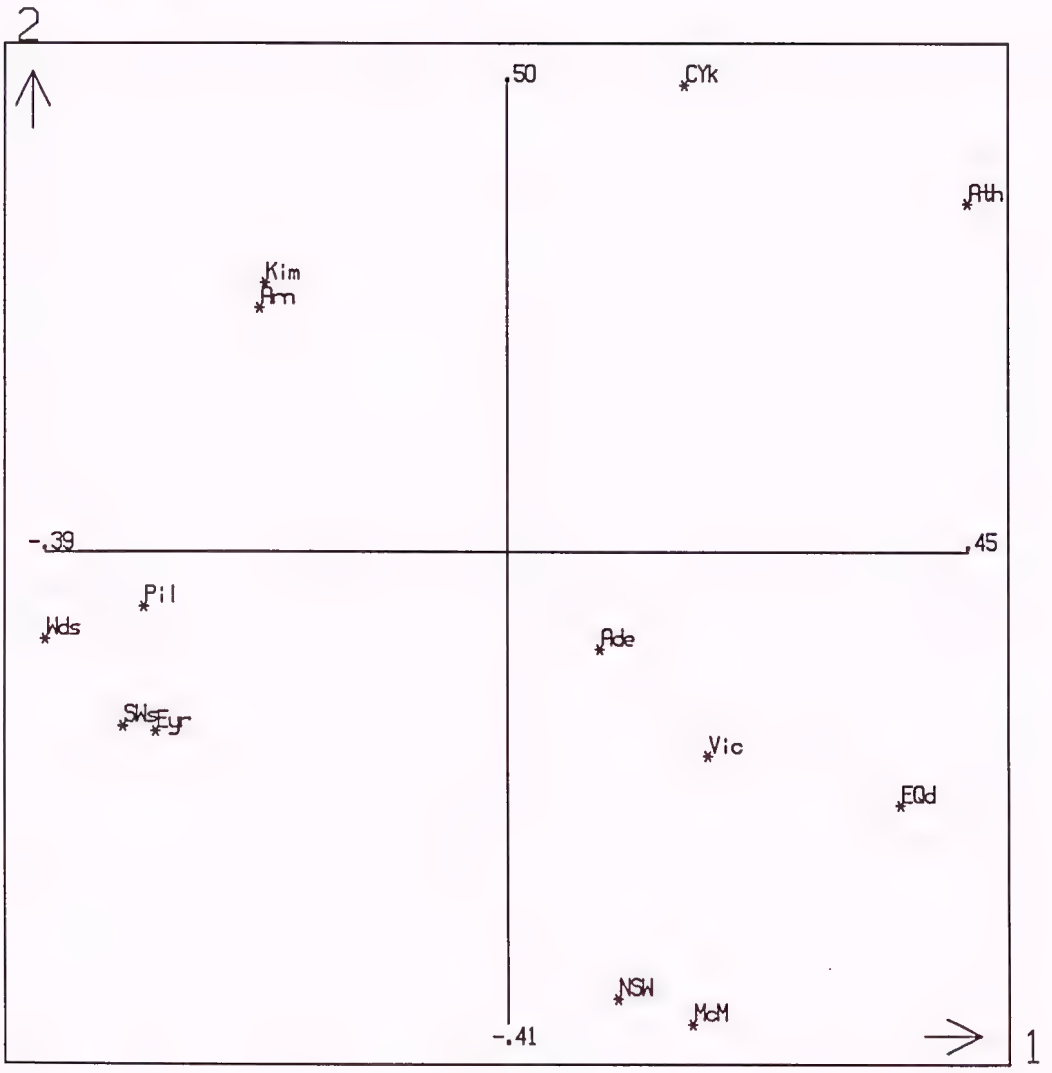


Figure 32. Ordination of provinces on PCA axes 1 and 2 from data in Table 4. Province codes as in Table 4.

Despite these problems, interesting results have been obtained by a purely phenetic analysis of the distributions of Australian ameniines. The starting point was the division of the continent into suitable provinces. For this I chose the recent scheme of Crisp *et al.* (1995), shown in Fig. 31, which incorporates those of earlier botanists, including the classical scheme of Burbidge (1960). It also closely resembles my own scheme (Colless, 1980), based on distributions of Australian Sepsidae (Diptera), and that of Cracraft (1991), based on avian distributions. Due to lack of records from the Northern Desert and Eastern Desert provinces of Crisp *et al.*, those provinces were omitted in the analysis that follows. New Guinea was not considered further, but its close relationship to the Cape York province is demonstrated by the sharing of the genera *Stilbomyella* and *Paramenia* and two species of *Platytropesa*.

Table 4 shows the distributions of ameniine species over these provinces. Seven species were omitted because they are known from only one province and therefore provide little information, as well as causing numerous embarrassing ties in the phenetic analyses. These "presence-absence" data were subjected to a principal component analysis, which provided the ordination shown in Fig. 32. As shown there, component I crisply divides the continent east-west, along about longitude 138°E; component II likewise divides it north-south along about latitude 20°S. These relationships are also found by computing Manhattan distances between provinces, and from these a minimum spanning tree (Fig. 33). I should stress that these computations treat absence of a species as just as significant as presence (a point hotly contested in various contexts, and one I have no intention of arguing here). The point remains: granting the validity of the results, about which I have no qualms, how are they to be explained?

For a start, there is considerable agreement with the results of Crisp *et al.* (1995), which were based on congruence of cladograms for a number of plant genera. My Figs 32 and 33 show groupings of Southwest + Western Desert, Kimberley + Arnhem, Southeast NSW + McPherson-Macleay, and one of all the eastern and southeastern areas, from Adelaide to Atherton. These all appear in Crisp *et al.* (1995) figure 2 (which omits Eyre

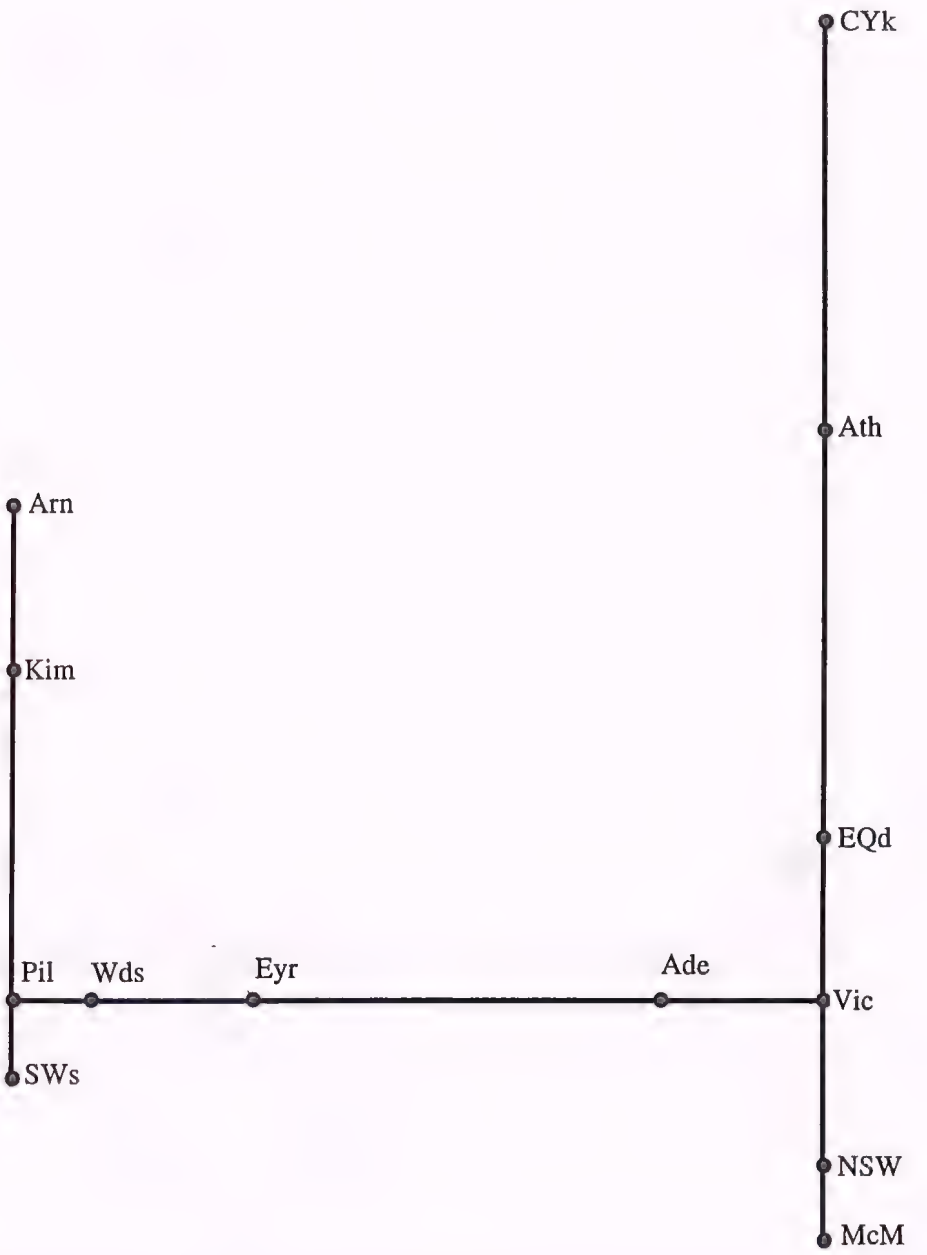


Figure 33. Minimum spanning tree from data in Table 4. Province codes as in Table 4. Arn and Kim are interchangeable due to a tie in distances.

and Pilbara). The notable difference is their grouping of Cape York with Arnhem and Kimberley, rather than Atherton; but my results do agree with those of Ovenden *et al.* (1987) for the bird genus *Platycercus*, which link Cape York with Atherton. The same can also be seen in the results of Cracraft (1982) for a number of bird genera. It is clear, then that ameniines generally have followed an ancient pattern of dispersal that occurs widely in both plants and animals.

It is also clear from (especially) the ordination (Fig. 32) that the overall pattern is primarily geographic: excluding points NSW and McM, the envelope of the remaining points is a tolerable, albeit distorted, map of the Australian coastline! That is, species are shared between provinces to a considerable extent because of simple, geographic propinquity. This is scarcely surprising, but the very obvious distortions must then be explained some other way. For instance, the wide gap between Pilbara and Arnhem provinces seems to reflect the strong barrier to dispersal raised by the Great Sandy Desert—perhaps not just to dispersal of the flies themselves, but also of appropriate snail hosts. On the other hand, the large gap between Atherton and East Queensland provinces seems, on examination of records, largely due to the failure of New Guinea-linked species of *Platytropesa* (perhaps late arrivals) to penetrate southward, and of *Amenia dubia* to advance northward. The latter may represent a lingering trace of a vicariance barrier between *A. dubia* and the closely related *A. imperialis*. Likewise, the anomalous position of NSW and McM provinces is due largely to the

Table 4. Distribution of selected ameniine species over provinces shown on Fig. 31. **ADE**—Adelaide; **ARN**—Arnhem; **ATH**—Atherton; **CYK**—Cape York; **EQD**—Eastern Queensland; **EYR**—Eyre; **KIM**—Kimberley; **MMO**—McLeay-McPherson; **NSW**—Southeastern NSW; **PIL**—Pilbara; **VIC**—Victoria; **WDS**—Western Desert. Species codes as for Fig. 28.

Species	Province												
	KIM	ARN	CYK	SWS	PIL	WDS	EYR	ATH	EQD	ADE	VIC	NSW	MMO
P. semi	–	–	–	–	–	–	–	•	•	•	•	•	•
P. angu	–	–	–	–	–	–	–	•	•	–	–	–	•
St. cro	–	–	–	–	–	–	–	•	•	–	–	–	–
Pl. aur	–	–	•	–	–	–	–	•	–	–	–	–	–
Pa. arg	–	–	•	–	–	–	–	•	–	–	–	–	–
Pa. tro	•	–	–	–	–	–	–	•	–	–	–	–	–
Am. imp	–	–	•	–	–	–	–	•	•	•	•	•	•
Am. alb	•	•	–	–	–	–	–	–	–	–	–	–	–
Am. cri	–	–	•	–	–	–	–	•	–	–	–	–	–
Am. dub	–	–	–	–	–	–	–	–	•	–	•	•	•
Am. mac	–	–	–	•	–	–	•	–	–	–	–	•	•
Am. leo	•	•	•	–	–	–	–	•	•	•	•	–	–
Am. lon	–	–	–	–	–	•	•	–	–	•	–	–	–
Am. sex	–	•	•	–	–	–	–	–	–	–	–	–	–
Am. chr	–	–	•	–	–	–	–	•	•	•	•	•	•
Am. nig	–	–	–	•	•	•	–	–	–	–	–	–	–

well-known zoogeographic discontinuity in southeastern Queensland (Colless, 1994: 526) that separates the sister species *A. leonis* and *A. albomaculata* (and the morphometric forms of *A. chrysame* and *A. dubitalis*, noted in Part 1); also to the failure of *Stilbomyella crosskeyi*, with sister species in New Guinea, to penetrate further south. Finally, the gap between Adelaide and Eyre provinces seems mainly due to the failure of "eastern" species, such as *A. imperialis* and *A. chrysame* to disperse further westwards.

One final point: the weight of evidence seems to point overwhelmingly to the dispersal of *Amenia* spp., perhaps from Arnhem Land, or at least from Cape York, in a clockwise fashion around Australia. Not a single species is shared between the Pilbara and the Kimberleys, although the occurrence in the former of *Silbomyia palpalis* may represent a unique crossing of the Great Sandy Desert by the stock of the putative *Silbomyia*-like ancestor, now extinct in the area from which it entered Asia (or Australia!). Penetration of the interior seems to have been slight, involving only the northward extension of *A. longicornis* (Eastern form) and the southward extension of *Paraplatytropesa* (*P. parvifrons*), which meet in the vicinity of Alice Springs,

I have merely sketched some possibilities with respect to these intriguing patterns. There is a clear need for more rigorous investigation, including mathematical modelling of possible mechanisms. It does seem, however, that both dispersal and vicariant speciation have played a role in the distribution of Ameniinae in Australia.

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Appendix

Details of the 54 characters and their observed states, as used in numerical analyses, are given below and the character matrix is shown in Table 5. Characters nos. 4, 5, 6, 20, 53, and 54 are unordered; others are considered to be linearly ordered but not polarised; i.e., the numerical codings do not imply plesiomorphy or otherwise in the states coded (see also comments in text).

1 Ratio of head width to frons width, male: 1 = 3–5; 2 = 10-20; 3 = >20.
2 Apex of arista, male, reaching to: 0 = short of apex of A3; 1 = about level with apex of A3; 2 = a little past apex of A3; 3 = well past apex of A3.
3 Carina, separation from epistoma: 0 = none; 1 = slight; 2 = conspicuous.
4 Anterior surface of carina: 0 = more or less flattened; 1 = rounded; 2 = sharp.
5 Ventral half of carina, male (if flattened, refers to pollinose, flattened surface): 0 = more or less parallel-sided; 1 = tapering dorsad; 2= tapering ventrad.
6 As for 5, female.
7 Protrusion of carina in lateral view, male: 1 = at most very slight; 2 = moderate; 3 = conspicuous.
8 As for 7, female.
9 Orbital bristles, male: 0 = absent; 1 = present.
10 As for 9, female.
11 Prevertical bristle, male: 0 = absent; 1 = present.
12 Inner vertical bristles, female: 0 = more or less parallel; 1 = inclinate; 2 = decussate.
13 Outer vertical bristles, male: 0 = not developed; 1 = much shorter than inner; 2 = a little shorter than inner;
14 As for 13, female.
15 Ocellar bristles, male: 0 = not developed or exceedingly small; 1 = small to moderate; 2 = strong.
16 As for 15, female.
17 Extent of setulae on facial ridge, male: 0 = close to vibrissa only; 1 = up to 1/4 of ridge; 2 = about 1/2 of ridge; 3 = over 1/2 of the ridge.
18 As for 17, female.
19 Insertion of vibrissa with respect to margin of epistoma: 0 = about level; 1 = a little above; 2 = well above; 3 = far above.
20 Eye margins in facial view, female: 1 = more or less regularly diverging; 2 = more or less parallel; 3 = parallel along frons, then diverging.
21 Gular region: 0 = normal; 2 = slightly swollen; 3 = markedly swollen.
22 Hairs of dorsal occiput: 1 = pale; 2 = dark.
23 Hairs on gena: 1 = pale; 2 = dark.
24 Dorsal postorbital strip, male: 0 = normal; 1 = reduced but not obliterated; 2 = median part obliterated.
25 Humeral, notopleural, and subalar pale spots on thorax: 0 = absent; 1 = present.
26 Prealar pale spot on thorax: 0 = absent; 1 = present.
27 Presutural dorsocentral pale stripes on thorax: 0 = absent; 1 = present.
28 Broad pale sheen over presutural area of thorax: 0 = absent; 1 = present.
29 Notopleural setulae: 0 = few, confined to around bases of bristles; 1 = extending a little on to disc; 2 = extending broadly across disc.
30 Posthumeral bristle: 0 = absent; 1 = present.
31 Posthumeral bristle with respect to presutural bristle: 0 = laterad or more or less level; 1 = distinctly mesad.
32 Number of scutellar marginal bristles: 1 = 6; 2 = 8; 3 = >8.
33 Subscutellar setulae: 0 = confined to lateral margin; 1 = extending to a point short of second-last marginal bristle; 2 = extending to or a little past second-last marginal bristle; 3 = forming a complete band.
34 Suprasquamal ridge: 1 = bare; 2 = with small tuft of setulae adjacent to scutellum.
35 Propleuron: 0 = bare; 1 = setulose.
36 Posterodorsal strip of hind coxa: 0 = bare; 1 = with a few setulae; 2 = strongly setulose.
37 Fore tibia, *pd* setae: 0 = absent; 1 = present.
38 Mid tibia, number of *ad* setae: 1 = 1–2; 2 = 2–3; 3 = 3–4; 4 = 4 or more.
39 Mid tibia, number of *pd* setae: 1 = 1; 2 = >1.
40 Hind tibia, apical *pv* seta: 0 = absent; 1 = present.
41 Wing, ventral surface of 3rd costal sector: 0 = bare; 1 = setulose.
42 Costa of male wing: 0 = normal; 1 = conspicuously bowed anteriorly.
43 Distance from bend of vein M to crossvein i-m as compared with distance of bend to wing margin: 0 = greater; 1 = about equal; 2 = less.
44 Crossvein r-m: 0 = before middle of discal cell; 1 = at middle of cell.
45 Setulae at base of vein R_{3+4}: 0 = few only, confined to thickened boss; 1 = extending up to 1/4 distance to crossvein r-m; 2 = extending more than 1/4 distance to r-m.
46 Posterior margin of lower calypter: 0 = rounded; 1 = more or less straight but internal angle not produced; 2 = internal angle produced to fit beneath suprasquamal ridge.
47 Submedian marginal bristles on abdominal T3, male: 0 = none; 1 = 1 pair; 2 = usually with 4 or more.
48 As for 47, female.
49 Dorsal marginal bristles on abdominal T4: 1 = up to 10; 2 = usually >10.
50 Pale lateral spots on abdominal T3: 0 = none; 1 = very small; 2 = moderate but confined to lateral area; 3 = extending on to dorsum; 4 = forming a complete dorsal band.
51 Pale submedian markings on abdominal T3: 0 = absent; 1 = paired spots; 2 = complete dorsal band.
52 Pale lateral spots on abdominal T5: 0 = none; 1 = very small; 2 = moderate but lateral only; 3 = extending on to dorsum.
53 Setae on abdominal S2–4, male: 0 = short hairs only; 1 = spiny hairs; 2 = long fine hairs; 3 = as 2 but extremely bushy.
54 As for 53, female: 0 = short hairs; 1 = strong bristles; 2 = strong spines.

Table 5. States of 54 characters (see Appendix) for 26 species of Ameniinae and two outgroups. For species codes, see Fig. 28 (p. 114).

Species	Characters 1–54					
P.semi	23????0001	0202221123	1210110121	0121010210	0020020022	0312
P.angu	33????0001	0202220123	0211110121	0121010110	0020020021	0312
S.mino	?212?1?1?1	??1?2?111	111?110100	?110111??1	1?01211110	02?2
S.palp	12100?2?2?	1??2?2?0?1?	1110110100	?110110311	1000021113	001?
St.ano	?221?0?3?1	??2?2?0?111	0?1?000010	?1?0010221	1?11111111	01?2
S.mack	?221?1?2?1	?0?2?2?122	111?110101	1110111321	1?01211113	03?2
St.cro	2220003101	0202001121	1210000011	1130010111	0011011111	0131
St.nit	2320112201	0202001121	1220000011	1130010111	0011011110	0031
St.nig	2320112201	0202001131	1210000001	1130010211	0011011110	0031
Pl.aur	1020012221	1233222223	1110000021	1110111221	0011211110	0032
Pl.sim	1020012201	1223223231	1110000011	1110121221	0011211110	0032
Pa.arg	1211113221	1233223222	2220110101	1110101111	0011211111	0112
Pa.rie	1000112221	1022222202	2220110101	1110100111	0021011110	0022
Pa.par	1222333301	1022121002	1220100100	?110000111	0020011111	0022
Pa.tro	1000111021	1022223202	2220110100	?100110111	0021011110	0022
Pa.gra	1111210021	1011220112	2220100100	?100110111	0021201111	0022
Am.imp	1220002202	0111221131	0110110111	1211120221	0110121022	0312
Am.alb	1020002202	0112221131	0110110111	1211120211	0100121123	0312
Am.cri	1210002202	0112221131	0110110111	1211120321	0100120020	0312
Am.dub	1310002202	0112221131	0110110111	1221120321	0110121022	0312
Am.mac	3320002102	0112221131	0112111021	1111120211	0010121122	1212
Am.leo	2220002202	0102221131	0111111021	1111110211	0010120022	1212
Am.lon	1020222202	0112221131	0110111001	1210110421	0120021123	0312
Am.sex	2120222202	0102111131	0110010121	1321110311	0000121121	1312
Am.chr	2230222201	0202122131	1112111001	0110110111	0010022123	0312
Am.nig	2220222201	0202222231	0111111011	1321110321	0020022224	2412
Phumos	33???????01	0202020103	0112000131	2120120110	1001210020	0000
Euphum	33???????01	0203121123	0112000020	?131121110	1000020024	2400

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A Revision of the Genus *Minibiotus* (Tardigrada: Macrobiotidae) with Descriptions of Eleven New Species from Australia

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ABSTRACT. The genus *Minibiotus* is redefined and the type species, *Minibiotus intermedius* (Plate, 1889) is redescribed. Eleven new species of *Minibiotus* are diagnosed and described, and three are transferred from the genus *Macrobiotus* using a range of qualitative and quantitative characters of adults and eggs. Keys are provided to the adults of the 22 reported species in the genus and to the eggs of the 20 species for which eggs have been described. Characters useful in discriminating species with very similar morphology are noted. The difficulties inherent in taxonomic studies of small animals such as many of those in the genus *Minibiotus* are discussed as are the problems of recognition of species in groups where both the adult form and sometimes also the egg are very similar. The examination and description of the eggs is important in tardigrade taxonomy.

CLAXTON, SANDRA K., 1998. A revision of the genus *Minibiotus* (Tardigrada: Macrobiotidae) with descriptions of eleven new species from Australia. *Records of the Australian Museum* 50(2): 125–160.

Minibiotus Schuster *et al.*, 1980 is a genus of terrestrial tardigrades found commonly in mosses and lichens. The type species *Minibiotus intermedius* (Plate, 1889) remained the only species in the genus until *M. macularta* was described by Pilato & Claxton in 1988. The adults of this species closely resembled *M. intermedius* but the eggs were quite dissimilar, having processes that lacked an enclosing membrane—a character suggested as definitive for the genus by its authors. Further species have since been described. *Minibiotus fallax* was described by Pilato *et al.* in 1989. This species had few adult characters similar to those of *M. intermedius* apart from the presence around the mouth of papulae (Fig. 1a) rather than the lamellae present in the closely related genus *Macrobiotus*. Miller *et al.*, (1994) transferred *Macrobiotus weinerorum* Dastych, 1984 to the genus *Minibiotus* while Dastych & Drummond (1996) attributed *Macrobiotus stuckenbergi* Dastych *et al.*, 1990 to the genus *Minibiotus*. Binda & Pilato (1992) described two new species and transferred *Macrobiotus furcatus* to the genus *Minibiotus*. They suggested that the *Minibiotus* bucco-pharyngeal apparatus has a "characteristic appearance" which includes double curvature of the buccal tube, stylet supports inserted a considerable distance from the pharyngeal bulb and first macroplacoid situated very close to the apophysis. The genus *Minibiotus*, however, has not been uniformly accepted (Ramazzotti & Maucci, 1983) perhaps because of its unsatisfactory definition (Pilato, 1982). One of the aims of this paper is to provide a more precise definition of the genus.

Minibiotus intermedius (Plate, 1889) itself, is considered to be a cosmopolitan tardigrade, having been reported from many countries (McInnes, 1994). The original description of specimens from Chile and Marburg, Germany (the exact type locality was not noted), like most supplied in those times, is inadequate by today's standards, lacking illustrations and mention of the egg. The species however, seems to have been readily recognized by many workers even before Thulin (1911) provided a more complete description of the animal and its egg from material collected in Europe. A review of the extensive literature on this species, in which many authors cite its presence in many countries, reveals that most citations are based on the "characteristic appearance of the adults" usually with no reference to the egg. Another aim of this work was to obtain specimens identified as *M. intermedius* from as many countries as possible to determine if there is a single cosmopolitan species which conforms to the description of this species and, more importantly, has a set of clearly definable characters.

The work presented here is part of a study of the Australian terrestrial tardigrade fauna and it has been found that specimens with the characteristic appearance of *M. intermedius* are frequently encountered and abundant in mosses and lichens. Close examination of these and careful collection of eggs with specimens have revealed that although many could be mistaken on adult morphology for *M. intermedius* as described by Thulin (1911), they have very different egg types. In this paper eleven new species are described and three are transferred from the genus *Macrobiotus* based on a character set which includes new quantitative and qualitative characters of adults and eggs. Keys are provided to the adults and to the eggs of these and the eight previously described species in the genus.

Materials and methods

Tardigrades were extracted from mosses and lichens from many localities in Australia. The sample of cryptogam was placed in about 750 ml of tap water in a beaker and left to soak for about eight hours or overnight. The sample was agitated and then squeezed over the beaker and removed. Water and sediment were poured through a coarse sieve (about 2 mm mesh) and then through a fine sieve (40 µm) using boiling water in the latter case. The sediment on this mesh was washed into a Petri dish and individual animals and eggs removed to mounting medium with an Irwin loop. Individual specimens were mounted in Hoyer's medium on microscope slides and the coverslip sealed with epoxy paint after three weeks drying. Measurements were made at the highest power (×1250) using an Olympus BH microscope equipped for oil immersion phase contrast microscopy, an eyepiece micrometer and a drawing tube. Some specimens were examined using Nomarski (or DIC) microscopy. Other specimens were gold coated for scanning electron microscopy studies.

Body lengths were measured from the mouth to the end of the body, not including the back legs. Buccal tube lengths were measured from the stylet sheaths to the base of the tube. Buccal tube widths were measured as the external diameters of the buccal tubes at the level of the stylet support insertion point. In all species the buccal tube walls were found to be 0.5 µm thick. Lengths of claws were measured from the base of the claw to the top of the main branch, excluding the accessory claw. The *pt* ratio (Pilato, 1981) is the ratio of the length of a given structure to the length of the buccal tube expressed as a percentage. Abbreviations used in tables include: BT—buccal tube, m—macroplacoid, MPR—macroplacoid row, PH—pharyngeal bulb, PR—placoid row, SI—stylet support, and VS—ventral support.

Eggs were ascribed to new species only after observation of an embryonate egg. A "specimen" in the text below implies an adult specimen.

All holotypes and some paratypes are deposited in The Australian Museum, Sydney. Other paratypes and other material are in the author's collection (SKC). Other material (slide mounted specimens) was borrowed from a number of institutions and private collections. These are listed below and referred to in the text by their abbreviations:

AM	Australian Museum, Sydney
BG	collection of Mr B. Grabowski, Marburg, Germany
BMD	Bohart Museum, University of California, Davis, USA
MM	Macleay Museum, University of Sydney
MUT	Department of Biology, McMurry University, Texas, USA
NM	collection of Mr N. Marley, Bristol, United Kingdom
NMP	Natal Museum, Pietermaritzburg, South Africa
NZM	Museum of New Zealand, Wellington, New Zealand
UCI	Dipartimento di Biologia Animale, Universita di Catania, Catania, Italy
UMI	Dipartimento di Biologia Animale, Universita degli Studi di Modena, Modena, Italy
UNP	Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina
VB	collection of Dr V.I. Biserov, Institute of Inland Water Biology, Yaroslavl District, Russia
WM	collection of Dr W.R. Miller, Kansas, USA
ZIM	Zoologisches Institut und Museum, Hamburg University, Hamburg, Germany

Systematic account

Genus *Minibiotus* Schuster *et al.*

Minibiotus Schuster, Nelson, Grigarick & Christenberry, 1980: 294.

Type species. *Macrobiotus intermedius* Plate, 1889: 535.

Diagnosis. Macrobiotidae with ten peribuccal papulae, no peribuccal lamellae. Antero-ventral mouth; teeth in oral cavity absent or strongly reduced. Buccal tube short, rigid; narrow (12% or less of buccal tube length); wall thickened below point of insertion of stylet supports; stylet supports inserted at 73% or less of buccal tube length; ventral support short (62% or less of buccal tube length) and macroplacoid row length 42% or less of buccal tube length.

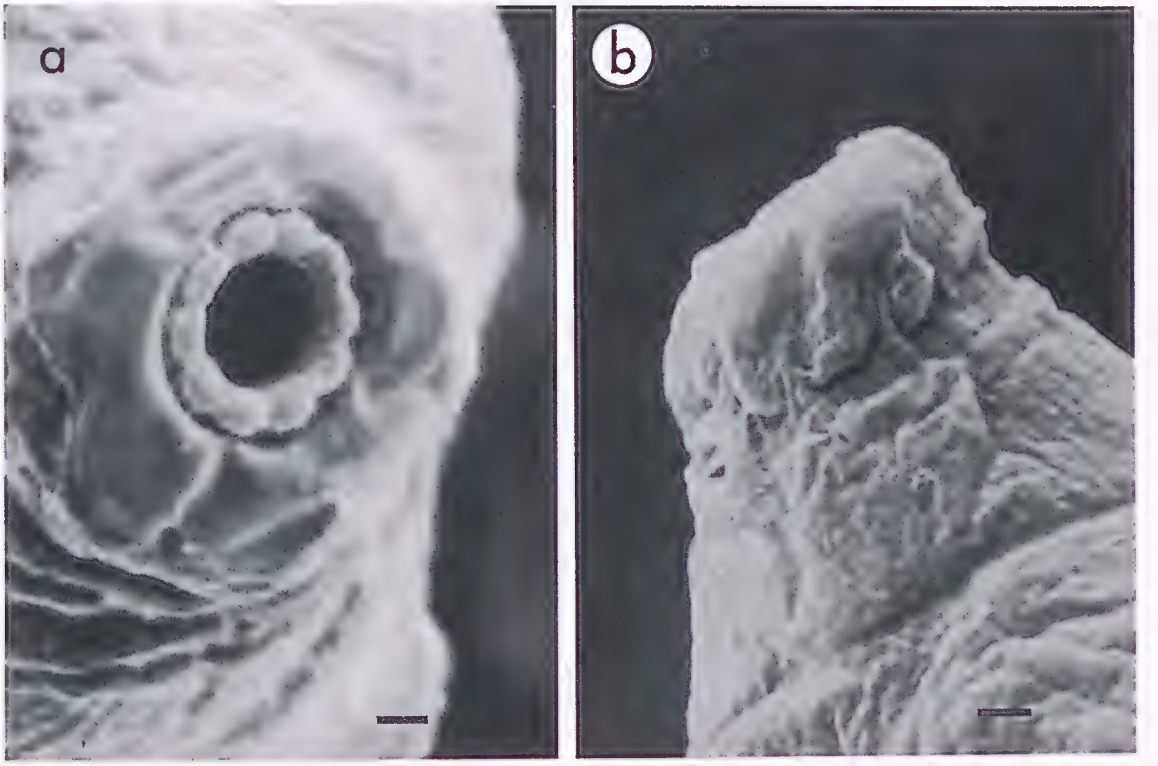

Figure 1. **a**, papulae of *Minibiotus hufelandioides* SEM; **b**, suboral pores of *Minibiotus aculeatus* SEM. (Scale bars = 1 μm).

Keys to species of *Minibiotus*

Key to adults

1 two macroplacoids 2
—— three macroplacoids 3

2 cuticle with dorsal tubercles especially towards rear ..... *M. fallax*
—— cuticle without dorsal tubercles ..... *M. scopulus*

3 cuticle with pores 4
—— cuticle without pores 14

4 pores in rows 5
—— pores randomly distributed 9

5 cuticle thickened in caudal region ..... *M. ethelae*
—— no caudal thickening 6

6 pores irregular in size and shape 7
—— pores small and round 8

7 no granulation around claws ..... *M. furcatus*
—— granulation around claws ..... *M. bisoctus*

8 eight rows of small (0.5 μm) pores ..... *M. poricinctus*
—— ten rows (1.0 μm) pores ..... *M. keppelensis*

9 soft spines above leg IV, or above legs II, III and IV ..... *M. aculeatus*
—— no soft spines 10

10 granulation on fourth pair of legs only ..... *M. asteris*
—— granulation on all legs 11

11 dorsal crest in oral cavity fragmented into teeth ..... *M. vinciguerrae*
—— no teeth in oral cavity 12

12 teeth on lunules of fourth pair of legs ..... *M. stuckenbergi*
—— no teeth on lunules of fourth pair of legs 13

13 long macroplacoid row; short, low accessory claws ..... *M. ramazzottii*
—— short macroplacoid row; very high accessory claws ..... *M. weinerorum*

14 cuticle with transverse rows of wrinkles ..... *M. pilatus*
—— cuticle smooth 15

15 granulation around claws absent or very sparse ..... *M. intermedius*
—— granulation around all claws 16

16 macroplacoid row length long (*pt* greater than 36) 17
—— macroplacoid row length short (*pt* less than 35) 19

17 stylets inserted at *pt* 73 ..... *M. milleri*
—— stylets inserted at *pt* less than 73 18

18 ventral reinforcing bar long (*pt* 53), claws long (*pt* IV pair 34.6) ..... *M. aquatilis*
—— ventral reinforcing bar short (*pt* 46), claws short (*pt* IV pair 293) ..... *M. hufelandioides*

19 toothed lunules on IV claws, short high accessory claws ..... *M. maculartus*
—— smooth lunules on IV claws 20

20 stylets inserted at *pt* 60.3; short, low accessory claws ..... *M. taiti*
—— stylets inserted at *pt* greater than 60.3 21

21 claws long (*pt* IV pair 34.0), high accessory claws ..... *M. floriparus*
—— claws short (*pt* IV pair 28.1), low accessory claws ..... *M. hispidus*

Key to eggs

1 processes with membrane 2
—— processes without membrane or with partial membrane 5

2 membrane covering thin nail-like processes ..... *M. taiti*
—— membrane enclosing each process separately 3

3 processes shaped like short-stemmed flowers ..... *M. floriparus*
—— processes shaped like screw-heads 4

4 processes small, height 2.5–3.5 µm, top 2.5–3.5 µm, 3–4 µm apart ..... *M. intermedius*
—— processes height 6.5–7 µm, top 5.5 µm, 6–8 µm apart ..... *M. poricinctus*

5 processes partially enclosed by membrane 6
—— processes without membrane 8

6 processes long, javelin-shaped, protruding through membrane and arranged in rings, others short rods ..... *M. pilatus*
—— processes cone-shaped 7

7 processes short cones with large pores around wide base, membrane reaching only to top of pores ..... *M. keppelensis*
—— processes long cones tapering to blunt tip, indented base enclosed in membrane ..... *M. milleri*

8 processes in form of inverted chalice 9
—— processes cone-shaped or hemispherical 10

9 distal disk of processes with smooth or slightly notched margin, shell dotted ..... *M. hufelandioides*
—— distal disk of processes with 6–8 distinct arms, shell smooth ..... *M. asteris*

10 processes hemispherical, shell surface smooth ..... *M. weinerorum*
—— processes conical or if hemispherical with longitudinal ridges around base 11

11 processes conical or hemispherical with longitudinal ridges around base ..... *M. maculartus*
—— processes elongated cones 12

12 processes fine and close; shell reticulate ..... *M. hispidus*
—— processes with conical or swollen base; shell smooth or dotted 13

13 smooth egg shell 14
—— dots on egg shell 16

14 processes base smooth, processes 3.5–5.5 µm long ..... *M. ramazzottii*
—— processes base indented 15

15 processes 8 µm long ..... *M. vinciguerrae*
—— processes 9–11 µm long ..... *M. aculeatus*

16 processes base indented; processes 11–12 µm long ..... *M. aquatilis*
—— processes base smooth 17

17 processes with round base rising rapidly to fine filamentous tip 18
—— processes strap-like variable in length, slightly swollen at base 19

18 processes 5–6 µm long ..... *M. furcatus*
—— processes 12–23 µm long ..... *M. ethelae*

19 processes 6–11 µm long, rarely up to 16 µm ..... *M. scopulus*
—— processes 12–16 µm long, rarely up to 22 µm ..... *M. fallax*

Species descriptions

Minibiotus intermedius (Plate, 1889)

Figs. 2, 18a; Table 1

Macrobiotus intermedius Plate, 1889: 535.

Type material examined. NEOTYPE in AM (AM KS41463): **Germany**: Marburg, 27 August 1994, B. Grabowski, moss on oak bark. SYNTYPES (3 specimens on 2 slides in AM): same data as neotype, AM KS41464–KS41465.

Material examined. AUSTRALIA: New South Wales: Cambewarra Mountain, 34°48'S 150°35'E, 625 m, 9 May 1993, S.K. Claxton, mosses and lichens on sandstone rock in cool temperate rain forest, 8 specimens, 20 eggs. Burragorang, 34°04'S 150°26'E, 29 July 1990, R. Siebels, moss and lichen on rock in open forest, 5 specimens, 3 eggs. Blue Mountains, 33°43'S 150°20'E, 1200 m, 26 December 1993, S.K.C., moss and leaf litter in closed forest, 1 specimen. Douglas Park, 34°11'S 150°43'E, 110 m, 9 March 1986, 17 May 1986, 19 July 1986, 13 September 1986, 15 November 1986, 11 January 1987, S.K.C., mosses and lichens on sandstone in open forest, 60 specimens, 16 eggs. Barrengarry, 34°40'S 150°30'E, 26 December 1993, S.K.C., leafy liverwort on tree in cool temperate rainforest, 1 specimen. Wederburn, 34°10'S 150°50'E, 23 March 1993, lichen on rock in open forest, 1 specimen; *ditto* but collected 7 August 1993, S.K.C., moss on rock, log in sheltered gully, 2 specimens. Wombeyan, 34°19'S 149°58'E, 8 March 1992, S.K.C., moss and lichens on sandstone in open forest, 3 specimens, 2 eggs. Fitzroy Falls, 34°38'S 150°30'E, 26 January 1986, S.K.C., moss and lichens on dead trees in open forest, 2 specimens. New England National Park, 30°30'S 152°30'E, 1200 m, 20 April 1995, moss on rock in subalpine heath, 3 specimens; *ditto* but collected 7 January 1996, moss and lichen on rock in subalpine heath and open forest, 55 specimens, 7 eggs; *ditto* but collected 18 December 1994, S.K.C., moss and lichen on rock in open field, 15 specimens. Queensland: Cunningham's Gap, 28°03'S 152°25'E, 3 September 1985, liverwort on twigs in temperate rainforest, 3 specimens; *ditto* but collected 10 January 1996, S.K.C., lichen and leafy liverwort on branches, logs, rocks in temperate rainforest, 14 specimens, 1 egg. (All Australian specimens in SKC). NEW ZEALAND: North Island: Pilbrows Hill, 16 May 1971, D.S. Horning Jr, 1 specimen (NZ642); Rangatira Island, 25 August 1971, D.S. Horning Jr, 1 specimen (NZ893). (NZM). UNITED KINGDOM: Surrey: Bookham Common, P. Marley, 9 specimens. Devon: Plymouth, P. Marley, moss and lichen on oak, 1 specimen. Morwelham, P. Marley, moss and lichen, 3 specimens. (PM). NORTH AMERICA: Alaska, Denali National Park, P. Marley, 5 specimens. (PM). Michigan, Schoolcraft County, 14 August 1978, T. Hounseal, moss from base tree in virgin forest, 4 specimens. Tennessee, Henderson County, 2 August 1980, C.W. Beasley, lichen from tree, 4 specimens. Missouri, Carter County, 1 August 1980, C.W. Beasley, lichen on oak tree and rock, 4 specimens. (MUT). SOUTH AMERICA: Venezuela, Obispos, Barrinas, 6 July 1979, R.W. Brooks, A.A. Grigarick, J. McLaughlin and R.O. Schuster, 4 specimens. Pedraza, Barinas, 4 July 1979, Brooks *et al.*, 9 specimens. Liberatador, Merida, 3 July 1979, Brooks *et al.*, 32 specimens. Girardot, Aragua, 14 July 1979, Brooks *et al.*, 2 specimens. Perija, Zulia, 24 June 1979, Brooks *et al.*, 1 specimen. (BMD). SOUTH AFRICA: Natal Midlands, Geckies Farm, 4 December 1988, P. Croeser, moss and fern in indigenous forest, 10 specimens and 1 egg. (NMP). ITALY: Sardegna, Caprera, 21 March 1974, R. Bertolani, lichen, 4 specimens. (UMI).

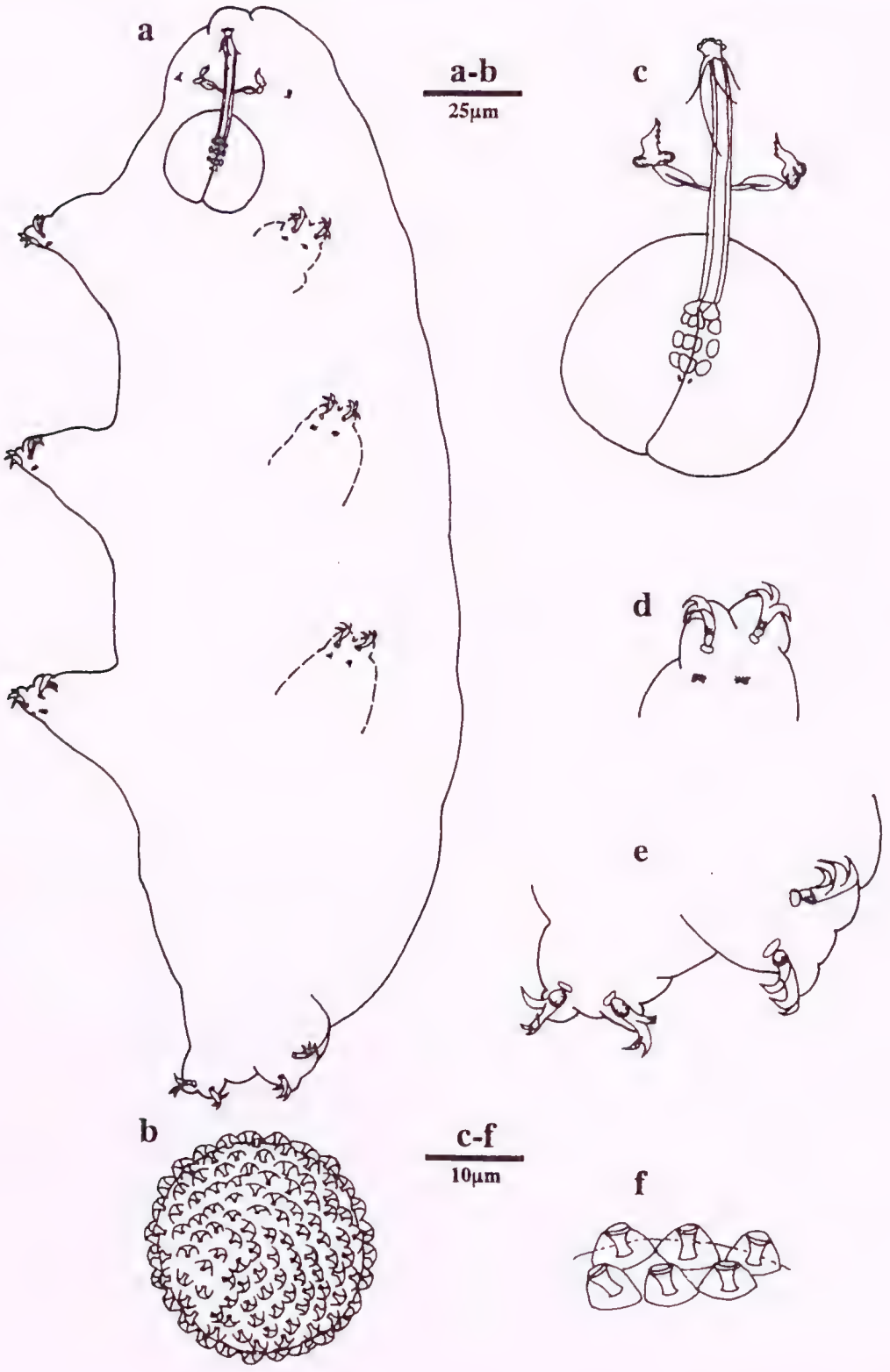

Figure 2. Taxonomic details of *Minibiotus intermedius*: **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Diagnosis. Cuticle smooth, no pores; 3 small, granular macroplacoids and an indistinct microplacoid; short, robust claws with high prominent accessory claws and smooth lunules.

Description. Length 132–290 µm colourless. Eyespots large in posterior position. Cuticle smooth, granulation, if present at base of claws on fourth pair of legs, very sparse. Buccal tube very narrow (6.8% of buccal tube length), diameter 1.5 µm. Stylet supports inserted at 55% of buccal

tube length; ventral support very short (37.3% of buccal tube length). Pharyngeal bulb round (23 µm diameter) containing large triangular apophyses, three macroplacoids and one microplacoid. Macroplacoid row short (26.5% of buccal tube length); first macroplacoid round, slightly elongated anteriorly where it lies very close to the apophysis, second and third macroplacoids round, same size as first. Microplacoid very small and indistinct, lying close to third macroplacoid. Claws robust but short with long secondary branch (fourth pair of claws is 24.8% of length of buccal tube) and large, round refractive zone at base. Accessory claws long, rising high above main branch. Lunules small and smooth on all claws. Some sparse granulation found on fourth pair of legs on some specimens.

Eggs colourless round, diameter without processes 40–45 µm, with processes 45–52 µm. About 30 processes around circumference, about 130 in hemisphere. Processes nail-like, each surrounded by membrane; height 2.5–3.5 µm, base 0.5–1.5 µm, top 2.5–3.5 µm, 3–4 µm apart. The top on each process appears to consist of a ring of tiny pores visible only under the highest power of magnification.

Table 1. Measurements (in µm) of adults of *Minibiotus intermedius*.

Character	No.	Range	Mean	SD	SE	Neotype
body length	20	195–270	219.4	21.1	4.7	250
BT length	20	22.7–27.6	24.7	1.3	0.3	23.8
BT width	20	1.4–2.2	1.7	0.2	0.04	1.6
SI length	20	12.4–14.9	13.6	0.7	0.2	13.0
VS length	20	8.7–10.8	9.2	0.5	0.1	8.1
PR length	20	6.2–8.1	7.2	0.5	0.1	7.6
MPR length	20	5.7–7.0	6.5	0.3	0.07	6.5
m1	20	1.4–2.2	1.6	0.2	0.04	1.6
m2	20	1.1–1.9	1.6	0.2	0.04	1.6
m3	20	1.1–1.9	1.6	0.2	0.04	1.6
microplacoid	20	0.4–0.8	0.5	0.1	0.02	0.5
PH length	20	20.0–27.0	23.6	2.2	0.5	23
PH width	20	21.0–28.0	23.4	2.3	0.5	27
claw I	20	4.3–6.0	5.0	0.4	0.09	4.9
claw II–III	20	4.9–6.5	5.5	0.4	0.09	5.4
claw IV	20	5.4–7.0	6.1	0.4	0.09	6.0

Remarks. Many early reports recorded this species without observing eggs. The species seems to be most often confused with a very similar species, the adult of which has pores in the cuticle, described from Europe (Morgan & King, 1976; Maucci, 1986; McInnes, 1991), the Americas (De Barros, 1942; Beasley, 1978) and personally observed on slides from Italy, Russia and South Africa. This species has not yet been found in Australia although the new species, *Minibiotus poricinctus*, is very similar. It has not been included in this paper as embryonate eggs have not been observed by this author.

The above description of *M. intermedius* was not based on type material which probably no longer exists. There are no collections of tardigrades in institutions in Marburg (B. Grabowski, pers. comm.), and no slides of Plate in Frankfurt or Hamburg institutions (H. Dastych, pers. comm.). It is impossible to determine the type locality from the original description since Plate referred to material collected in both Chile and Marburg, Germany. It seemed expedient, therefore, to redescribe the species using material which is both cosmopolitan and which most closely resembles the original description and to erect a neotype from material from Marburg.

Minibiotus taiti n.sp.

Figs. 3, 18b; Table 2

Type material. HOLOTYPE in AM (AM KS41430): Australia, New South Wales: Ryde, 33°48'S 151°04'E, 500 m a.s.l., 16 June 1993, S.K. Claxton, foliose lichen and leaf litter on asphalt. PARATYPES (7 specimens, 3 eggs in AM [AM KS41431–41440]; 31 specimens, 2 eggs in SKC): same data as holotype but collected on 3 May 1985 and 1 February 1992.

Additional material examined. New South Wales: Appin, 34°12'S 150°47'E, 29 August 1985, P.D. Claxton, weft moss on rock in open sclerophyl forest, 10 specimens, 3 eggs. Sandy Hollow, 32°22'S 150°34'E, 20 March 1993, S.K. Claxton, weft moss on rock in open sclerophyl forest, 22 specimens, 5 eggs. Queensland: Eumundi, 26°28'S 152°27'E, 20 December 1986, D.S. Horning, fruticose lichen on old bridge timber, wind exposed, 6 specimens, 3 eggs. Great Keppel Island, 23°10'S 150°58'E, 14 July 1993, P.D. Claxton, foliose lichen on rock, wind exposed, 3 specimens, 1 egg. Australian material in SKC. NEW ZEALAND: Snares Islands, Ho Ho Creek, 23 October 1972, D.S. Horning, 2 specimens (SA301). Mollymawk Bay, 30 January 1971, D.S.H., 2 specimens (SA26). Seal Point, 2 March 1972, D.S.H., 2 specimens (SA216). Broughton Island, 18 February 1971, D.S.H., 4 specimens (SA60). (NZM). CHINA: Quingdao, October 1994, N. Marley, moss, 6 specimens in NM. USA: Texas, Taylor County, 27 December 1989, C.W. Beasley, leaf litter on soil, 2 specimens in MUT.

Diagnosis. Smooth cuticle with no pores and granulation on all legs; 3 round macroplacoids and a distinct microplacoid; long slender claws with short, low accessory claws and smooth lunules.

Description. Body length 160–320 µm, colourless. Eye spots, when present, in posterior position. Cuticle smooth, patch of granulation on the outside of first three pairs of legs near claws, also on back and sides of fourth pair of legs. Buccal tube narrow (8% of buccal tube length). Stylet supports inserted at 60.3% of the buccal tube length, ventral support very short (40.3% of buccal tube length). Pharyngeal bulb round (25 µm diameter) containing large, granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.1% of buccal tube length); first macroplacoid round but slightly elongated anteriorly where it lies under the apophysis (which is about the same size), second macroplacoid small, granular; third macroplacoid granular but with a slight caudal bulb which curves towards midline. Microplacoid distinct, lying close to third macroplacoid. Claws long and slender (fourth pair of claws is 33.2% of length of buccal tube) with refractive zone at base and with short secondary branch. Accessory claws short and lie close

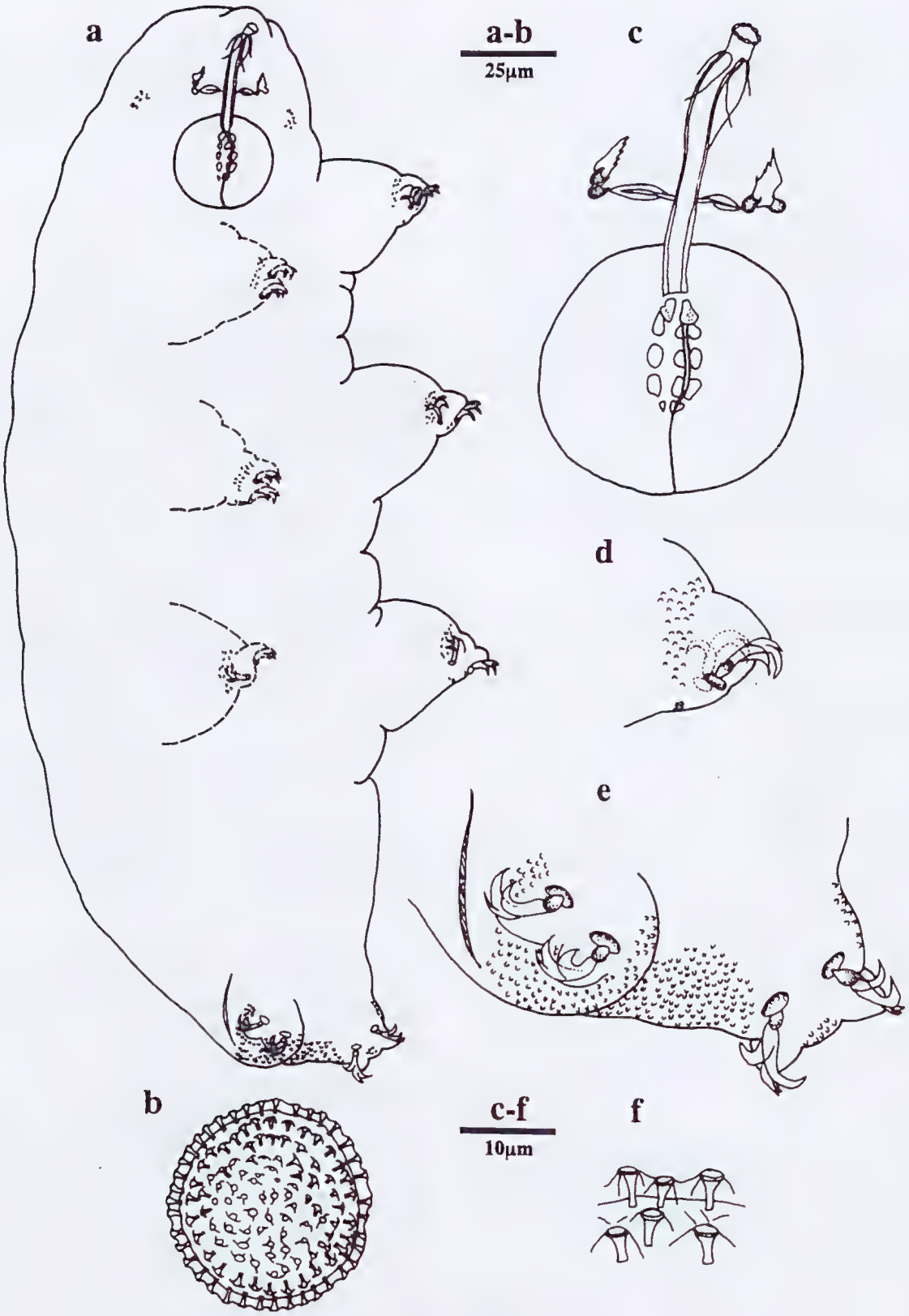

Figure 3. Taxonomic details of *Minibiotus taiti* n.sp.: **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

to main branch. Lunules smooth on all claws.

Eggs colourless, round, diameter without processes 54 µm, with processes 64 µm. About 48 processes around circumference, about 160 in a hemisphere. Processes like thin nails, 3.2–5.4 µm high, base diameter 1–1.5 µm, top diameter 2–3 µm. Top of each process appears to have a ring of very small circles around a central pore. A membrane surrounds each process but it is not clear if this is continuous over all the processes or if it reaches the shell surface between the processes.

Table 2. Measurements (in µm) of adults of *Minibiotus taiti* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	20	176–297	248	31.4	7.0	277
BT length	20	21.6–27.6	25.2	1.6	0.4	27.0
BT width	20	1.6–2.4	2.0	0.2	0.04	2.2
SI length	20	13.0–16.8	15.2	1.0	0.2	16.2
VS length	20	8.7–11.4	10.2	0.7	0.2	10.8
PR length	20	7.6–10.8	9.5	1.0	0.2	10.8
MPR length	20	6.5–9.2	8.1	0.9	0.2	9.2
m1	20	1.6–3.0	2.4	0.4	0.1	2.7
m2	20	1.6–2.7	1.9	0.3	0.1	2.2
m3	20	1.6–2.7	2.2	0.3	0.1	2.2
microplacoid	20	0.4–1.1	0.8	0.2	0.1	0.8
PH length	15	23.0–30.0	26.0	2.3	0.6	27
PH width	15	22.0–30.0	25.0	2.2	0.6	27
claw I	20	6.5–8.1	7.2	0.4	0.1	7.6
claw II–III	20	7.0–8.7	7.7	0.4	0.1	8.1
claw IV	20	7.6–9.2	8.4	0.6	0.1	9.2

Etymology. The species is named after Dr N.N. Tait of Macquarie University.

Remarks. This species differs from *M. intermedius* described above, by having granulation around the claws, a wider buccal tube, stylet supports inserted lower down the buccal tube and by the slightly different structure of the processes of the egg. It differs from *Macrobiotus acontistus* De Barros, 1942 by having a microplacoid, a narrower buccal tube, macroplacoids of similar size, the second never larger than the first and by having granulation around the claws.

Habitat. The type material was found in foliose lichens and *Eucalyptus* nuts on asphalt in the parking lot at Macquarie University. At other sites in NSW and in Queensland the species was found in mosses and lichens in locations subject to drying and high temperatures.

Minibiotus poricinctus n.sp.

Figs. 4, 18c; Table 3

Type material. HOLOTYPE in AM (AM KS41585): Australia, Tasmania: Mount Cameron West Aboriginal Site, 41°52'S 144°42'E, 9 January 1996, A. Moscal, moss on rock. PARATYPES (10 specimens, 3 eggs in AM [AM KS41586–41595]; 50 specimens, 5 eggs in SKC) same data as holotype.

Diagnosis. Cuticle with eight bands of small round pores and granulation on all legs; three round macroplacoids of the same size and an indistinct microplacoid; long slender claws with short, close accessory claws and thick smooth lunules.

Description. Body length 135–277 µm, colourless. Eye spots large in posterior position. Cuticle with eight bands of small, round (0.5 µm) pores around the body, sparse on the ventral surface and on the outside of all legs. Fine granulation on top and both sides of legs I–III just above claws, also around claws on leg IV. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 59.5% of buccal tube length, ventral support very short (35.8% of buccal tube length). Pharyngeal bulb almost round (24 µm long by 22 µm wide) containing large, triangular apophysis, three macroplacoids and a microplacoid. Macroplacoid row short (30.9% of buccal tube length); first macroplacoid slightly elongated anteriorly where it lies very close to and partly obscured by the apophysis; second and third macroplacoids round, same size as first. Microplacoid small and indistinct, lying close to third macroplacoid. Claws slender (fourth pair of claws is 27.3% of length of buccal tube) with long secondary branch and round refractive zone at base. Accessory claws short, lying close to main branch on all claws. Lunules small, smooth on first three pairs of legs, thick and smooth on fourth pair of legs.

Eggs round, diameter without processes 49 µm, with processes 60 µm. 18–20 processes around circumference, 50 in hemisphere. Processes screw-like, each surrounded by a membrane, height 6.5–7 µm, base 1.5 µm, top 5.5 µm, 6–8 µm apart. Small dots visible on shell surface around each process where membrane appears to reach the surface.

Etymology. Latin, *porus*, masculine, hole and *cinctus*, Latin noun, girdle, belt.

Remarks. The species is superficially very similar to *M. intermedius* and *M. taiti* but differs from them by the presence of bands of pores in the cuticle.

Habitat. The type material was found in a single mixed sample of two mosses (*Lembophyllum divulsum* and *Thuidium furfurosum*) and a liverwort (*Cheilolejeunea mimosa*) on a sandstone boulder in a littoral flat with low shrubs and herbs.

Table 3. Measurements (in µm) of adults of *Minibiotus poricinctus* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	20	174–290	240.3	30.0	6.7	270
BT length	20	20.5–28.1	24.7	1.6	0.4	26.0
BT width	20	1.5–2.2	1.9	0.2	0.04	2.1
SI length	20	12.2–16.8	14.7	1.0	0.2	15.4
VS length	20	7.6–10.3	8.8	0.6	0.1	9.2
PR length	20	7.0–10.0	8.7	0.7	0.2	8.7
MPR length	20	6.0–8.9	7.6	0.7	0.2	7.6
m1	20	1.6–2.5	2.1	0.2	0.04	2.2
m2	20	1.4–2.4	1.9	0.3	0.1	1.9
m3	20	1.4–2.4	1.9	0.3	0.1	1.9
microplacoid	20	0.5–1.0	0.6	0.2	0.1	0.5
PH length	15	20.0–27.0	24.0	1.9	0.4	25.0
PH width	15	20.0–26.0	22.7	1.8	0.4	24.0
claw I	20	4.3–6.2	5.6	0.5	0.1	6.0
claw II–III	20	5.1–6.8	6.2	0.4	0.1	6.5
claw IV	20	5.7–7.6	6.8	0.5	0.1	7.0

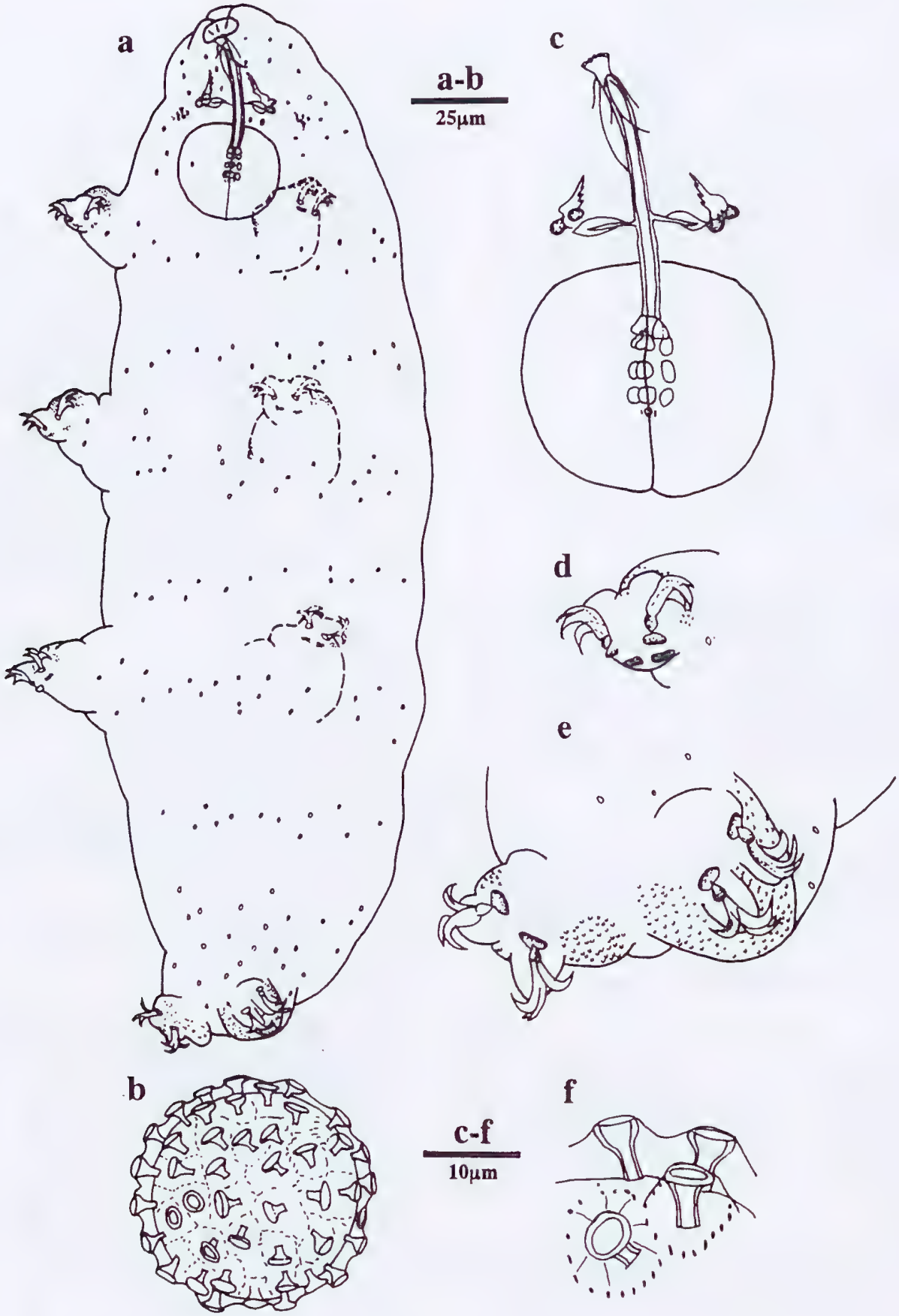

Figure 4. Taxonomic details of *Minibiotus poricinctus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

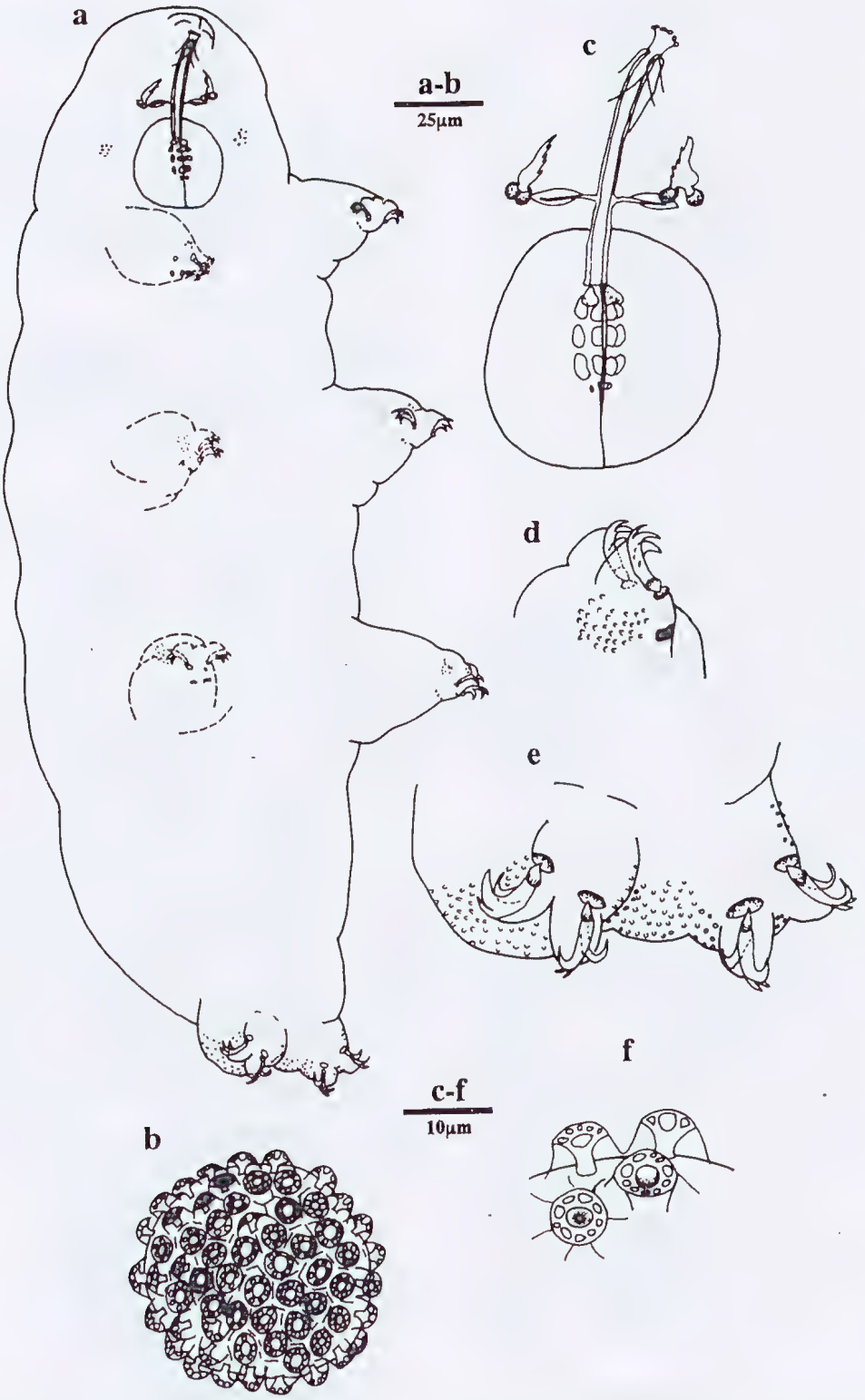

Figure 5. Taxonomic details of *Minibiotus floriparus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Minibiotus floriparus n.sp.

Figs. 5, 18d; Table 4

Type material. HOLOTYPE in AM (AM KS41441): Australia, New South Wales: Camden, 34°04'S 150°42'E, 120 m a.s.l., 4 April 1994, S.K. Claxton. PARATYPES (7 specimens, 5 eggs in AM [AM KS41442–KS41451]; 36 specimens, 8 eggs in SKC): same data as holotype.

Diagnosis. Smooth red-purple cuticle, granulation on all legs; three round macroplacoids of same size and a distinct microplacoid; long robust claws with short accessory claws which rise high above the main branch only on the fourth pair of claws and smooth lunules.

Description. Body length 152–420 µm, all but the smallest specimens with red-purple cuticle, some specimens also

Table 4. Measurements (in µm) of adults of *Minibiotus floriparus* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	19	170–420	300.2	64.9	14.9	285
BT length	19	20.0–33.5	27.1	3.6	0.8	27.6
BT width	19	1.6–2.7	2.1	0.4	0.1	2.1
SI length	19	13.0–21.6	17.5	2.4	0.6	17.8
VS length	17	9.2–16.2	12.5	1.7	0.4	13.0
PR length	19	7.6–14.1	10.7	1.9	0.4	11.4
MPR length	19	6.5–11.9	9.0	1.6	0.4	9.7
m1	19	1.9–3.8	2.7	0.5	0.1	2.7
m2	19	1.6–3.2	2.3	0.4	0.1	2.4
m3	19	1.6–3.8	2.6	0.5	0.1	2.7
microplacoid	19	0.4–1.5	0.8	0.3	0.1	0.8
PH length	17	21.0–32.0	26.9	3.4	0.8	27.0
PH width	15	22.0–38.0	27.5	5.0	1.3	24.0
claw I	19	5.4–10.3	7.8	1.4	0.3	7.6
claw II–III	19	6.0–10.8	8.3	1.3	0.3	8.1
claw IV	19	6.5–11.9	9.2	1.4	0.3	9.2

with purple granules. Eye spots large in posterior position. Cuticle smooth. Granulation on sides and back of first three pairs of legs above claws, granulation fine and dense on fourth pair of legs. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 64.4% of buccal tube length and ventral support long (46.1%). Pharyngeal bulb round (about 24 µm diameter) containing large granular apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row short (33.1% of buccal tube length); macroplacoids round granules of about the same size, second macroplacoid slightly smaller than other two, third with slight caudal bulb, which curves towards the midline. Microplacoid distinct and short. Claws robust (fourth pair of claws is 34% of length of buccal tube) with small refractive zone at base and with long secondary branch. Accessory claws short and rise high above the main branch on fourth pair of claws only. Lunules small and smooth on first three pairs of legs, thick and smooth on the fourth pair of legs.

Egg colourless, round, diameter without processes 62 µm, with processes 70 µm. 20–22 processes around circumference, 60–75 in hemisphere. Processes screw-shaped with flared distal end with ring of 9–10 pores around a central area, height 5.5–6 µm, base diameter 2–3 µm, distal disc diameter 6–7 µm. Each process surrounded by a membrane. Shell surface smooth.

Etymology. Latin, *floriparus*, bearing flowers, describing the egg and its processes.

Remarks. The species is very similar to *Minibiotus macularus* Pilato & Claxton, 1988, having a smooth cuticle and granulation around all claws but differs from it by having purple coloured cuticle, smooth lunules on the claws of the fourth pair of legs and also by having very different processes on the egg.

Habitat. The species was found only in crustose and foliose lichens on the branch of a species of *Eucalyptus* in open woodland.

Minibiotus aquatilis n.sp.

Figs. 6, 18e; Table 5

Type material. HOLOTYPE in AM (AM KS41452): Australia, Australian Capital Territory: Coppin's Crossing, 35°16'S 149°05'E, 1750 m a.s.l., 4 September 1993, S.K. Claxton. PARATYPES (7 specimens, 5 eggs in AM [AM KS41453–KS41462]; 23 specimens, 34 eggs in SKC): same data as holotype.

Additional material examined. NEW SOUTH WALES: Narrandera, 34°45'S 146°33'E, 19 March 1994, S.K. Claxton, lichen on rock in open forest, 22 specimens, 14 eggs. TASMANIA: King River, 42°00'S 145°32'E, June 1989, J. Lake, moss on rock, 3 specimens, 3 eggs. Mount Montgomery, 41°09'S 146°03'E, 21 October 1994, A. Moscal, moss on soil, 1 specimen. All SKC.

Diagnosis. Smooth cuticle with granulation on all legs; 3 long macroplacoids and a distinct microplacoid; long, slender claws with short, low accessory claws and toothed lunules on the fourth pair of claws.

Description. Body length 185–399 µm, colourless. Eye spots in the posterior position, consisting of large granules. Cuticle smooth, coarse granulation over back and both sides around claws on all legs. Buccal tube narrow (9% of buccal tube length). Stylet supports inserted at 68.3% of buccal tube length, ventral reinforcing bar 53%. Pharyngeal bulb round (about 30 µm diameter), containing large granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (37.9% of buccal tube length); first macroplacoid pear-shaped, lying close to apophysis and partly obscured by it, second macroplacoid granular, smaller than other two, third macroplacoid granular but with faint caudal knob turned towards midline. Microplacoid distinct, short and lies close to third macroplacoid. Claws long, slender (on fourth pair of legs, 34.6% of length of buccal tube) with large refractive zone at base and with short secondary

Table 5. Measurements (in µm) of adults of *Minibiotus aquatilis* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	16	182–399	309.8	55.6	13.9	354
BT length	16	21.6–36.8	31.0	4.1	1.0	35.7
BT width	16	1.8–3.5	2.8	0.4	0.1	3.2
SI length	16	14.6–24.9	21.2	2.9	0.7	24.9
VS length	15	11.4–20.0	16.6	2.3	0.6	18.9
PR length	16	8.7–19.8	14.0	2.0	0.5	16.8
MPR length	16	7.6–14.6	11.8	0.7	0.2	14.1
m1	16	2.2–4.3	3.5	0.7	0.2	3.8
m2	16	1.6–3.9	3.1	0.7	0.2	3.8
m3	16	2.2–4.3	3.4	0.7	0.2	4.3
microplacoid	16	0.6–1.9	1.3	0.4	0.1	1.6
PH length	11	22.0–43.0	33.0	5.4	1.6	36.0
PH width	11	22.0–43.0	33.0	6.1	1.9	35.0
claw I	16	6.0–10.3	8.9	1.2	0.3	9.7
claw II–III	16	6.5–10.8	9.4	1.2	0.3	10.3
claw IV	16	7.6–12.4	10.7	1.5	0.4	11.9

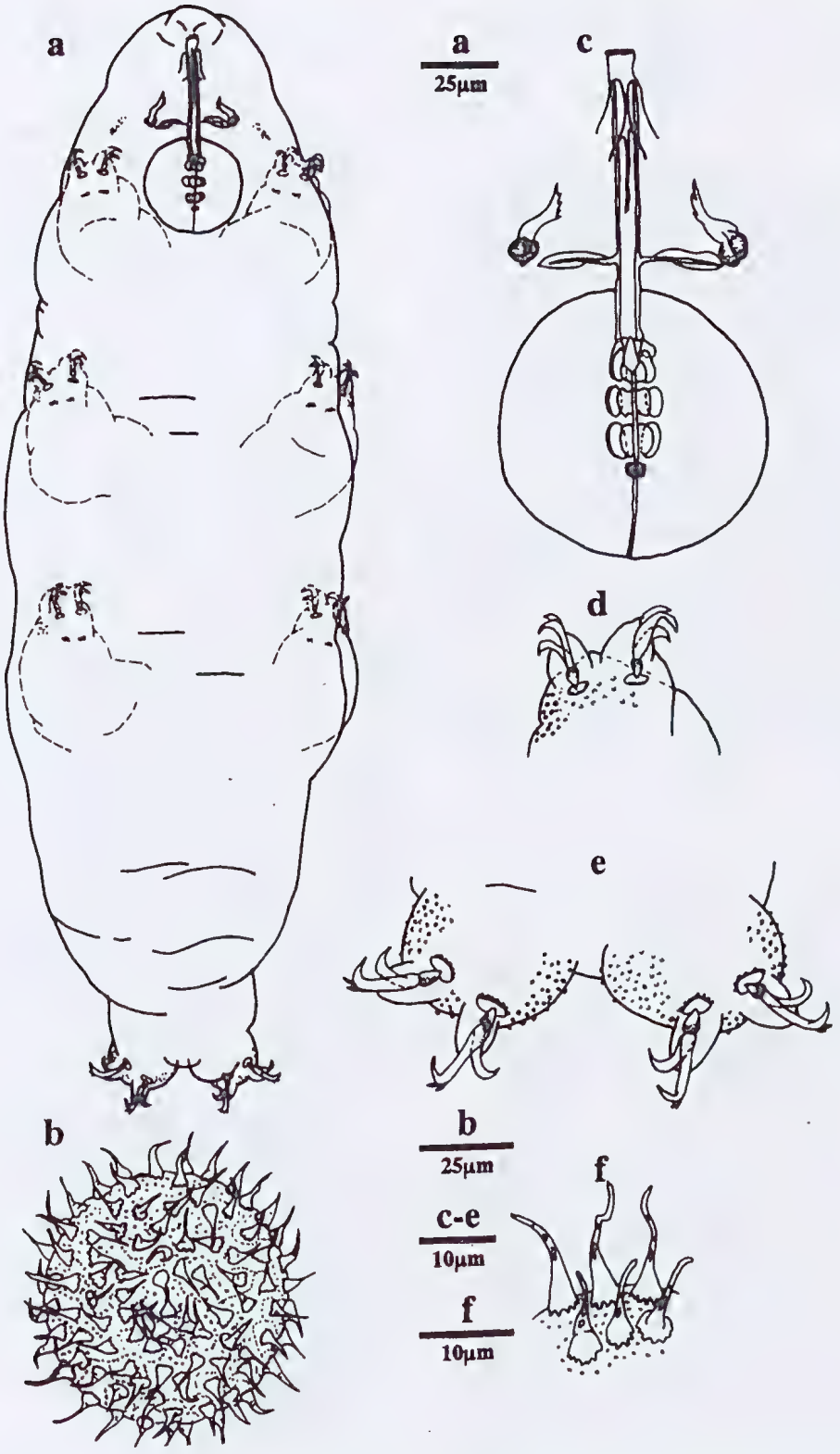

Figure 6. Taxonomic details of *Minibiotus aquatilis* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

branch. Accessory claws short and lie close to main branch. Lunules on first three pairs of legs smooth and distinct. Lunules on fourth pair of legs toothed.

Egg round, diameter without processes 60–70 µm, with processes 80–93 µm. Thirty-six processes around circumference, about 100 in hemisphere. Processes long cones tapering from hemispherical base (diameter 4–4.5 µm) to fine tip sometimes bifurcate, often terminating in several fine hairs. Tapering portion appears to have a single row of bubbles within it. Process height 11–12.5 µm (two eggs with processes 16–21 µm long), about 2 µm apart. Each process with indentations around the base. Shell

surface with large round dots around each process which may be difficult to see in some preparations.

Etymology. Latin, *aquatilis*, living near water, describing the type locality.

Remarks. The population from Narrandera differs from the type only by having more prominent eyes and shorter claws (relative to the length of the buccal tube). Eggs of the Narrandera population differ by having shorter, thinner processes than the type (8–9 µm long with base diameter 3–3.5 µm) and a little further apart (3 µm). However this is variable, one egg had process height 9–10 µm, base diameter 2–2.5 µm; two eggs had process height 5–7 µm, base diameter 3 µm. The dots around the processes are particularly clear in eggs from King River.

The species is similar to *Minibiotus macularta* Pilato & Claxton, 1988 and *Minibiotus floriparus* n.sp., having a smooth cuticle and granulation around all claws but differs from them in the position of insertion of the stylet supports and by having longer macroplacoids as well as having different shaped egg processes.

Habitat. The species was found in short turf moss and foliose lichens on rocks close to the Molonglo River at the type locality. At Narrandera it was found in very dry foliose lichens on rock in an open woodland and at King River in fine moss on rock.

Minibiotus hispidus n.sp.

Figs. 7, 18f; Table 6

Type material. HOLOTYPE in AM (AM KS41467): Australia, Queensland: Crow's Nest, 27°16'S 152°03'E, 3 September 1985, S.K. Claxton. PARATYPES (6 specimens, 4 eggs in AM [AM KS41468–KS41477]; 24 specimens, 5 eggs in SKC): same data as holotype.

Additional material examined. AUSTRALIA, New South Wales: Appin, 34°12'S 150°47'E, 29 June 1985, P.D. Claxton, moss and lichen on sandstone rock in open forest, 30 specimens, 5 eggs. Queensland: North Stradbroke Island, 27°30'S 153°30'E, 19 February 1996, R.M. Kristensen, soil under *Eucalyptus* tree, 10 specimens. Isla Gorge, 25°10'S 149°56'E, 7 March 1996, R.M. Kristensen, moss on rock, 8 specimens, 1 egg. Bribie Island, 27°30'S 153°08'E, 16 April 1995, S.K. Claxton, leaf litter and sand in *Banksia* heath, 21 specimens, 1 egg. Western Australia: John Forest National Park, 31°53'S 116°05'E, 22 November 1994, P.D. Claxton, moss and lichen on rock in open forest, 27 specimens, 1 egg. (All SKC). NEW ZEALAND: South Island, (NZ526) Canaan Rd, Abel Tasman National Park, 9 April 1971, D.S. Horning, 2 specimens in NZM.

Diagnosis. Smooth cuticle with granulation on all legs, 3 small round macroplacoids and an indistinct microplacoid; slender claws with short, low accessory claws and smooth lunules.

Description. Body length 160–350 µm, colourless. Eye spots in posterior position. Cuticle smooth, coarse granulation on top and sides of first three pairs of legs above claws and around claws on fourth pair of legs. Buccal tube narrow (8% of the buccal tube length). Stylet supports inserted at 65.2% of buccal tube length, ventral reinforcing bar very short, 45.7%. Pharyngeal bulb round (about 28 µm diameter) containing large granular apophyses, three granular macroplacoids and a microplacoid. Macroplacoid row short (33.2% of buccal tube length); macroplacoids almost equal in size, first somewhat pear-shaped, lying close to apophysis and partly obscured by it, second is granular and third granular with a faint caudal knob turned towards the midline. Small, indistinct microplacoid lies close to third macroplacoid. Claws slender (fourth pair of claws is 28.1% of length of buccal tube) with small refractive base and long secondary branch. Accessory claws short and rise high above main branch. Lunules on all claws small and smooth, somewhat thickened on fourth pair.

Eggs round, colourless, diameter without processes 59 µm, with processes 72 µm. 48 processes around circumference, about 340 in hemisphere. Processes small cones with fine tips, height 6.5–8.4 µm, base diameter 2.8 µm and 1–2 µm apart. Ring of very small pores around base of each process. Shell appears to be covered with very small pores of uniform size.

Table 6. Measurements (in µm) of adults of *Minibiotus hispidus* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	10	234–300	274.1	21.8	6.9	263
BT length	10	26.5–29.7	28.3	1.0	0.3	28.1
BT width	10	2.2–2.4	2.3	0.1	0.03	2.2
SI length	10	17.3–19.5	18.4	0.7	0.2	18.4
VS length	10	12.4–14.1	12.9	0.6	0.2	12.4
PR length	10	9.7–11.4	11.0	0.6	0.2	11.4
MPR length	10	8.7–9.7	9.4	0.4	0.1	9.5
m1	10	2.0–2.7	2.3	0.2	0.06	2.4
m2	10	1.6–2.2	2.0	0.3	0.09	2.2
m3	10	2.0–2.7	2.3	0.2	0.06	2.2
microplacoid	10	0.5–1.1	0.8	0.2	0.05	0.8
PH length	10	27.0–31.0	28.5	1.4	0.5	27.0
PH width	10	26.0–30.0	28.1	1.5	0.5	27.0
claw I	10	6.2–7.0	6.6	0.3	0.1	6.5
claw II–III	10	6.8–7.6	7.2	0.4	0.1	7.0
claw IV	10	7.3–8.7	8.0	0.4	0.1	8.1

Etymology. Latin, *hispidus*, bristly, prickly, describing the appearance of the egg.

Remarks. The population from Appin, NSW is smaller than the type population from Crow's Nest (mean body length 213.6 µm, SD 41.5 µm, n = 15) as is that from Perth (mean body length 196.9 µm, SD 36.4 µm, n = 16) but otherwise the adults are the same. Egg processes from the Appin population are slightly longer (10 µm) and further apart (3.3 µm) than those of the type population. The single egg from Perth has quite narrow processes (1.5–2 µm base diameter).

The species is very similar to *Minibiotus macularta* but has a shorter ventral support and smooth lunules on

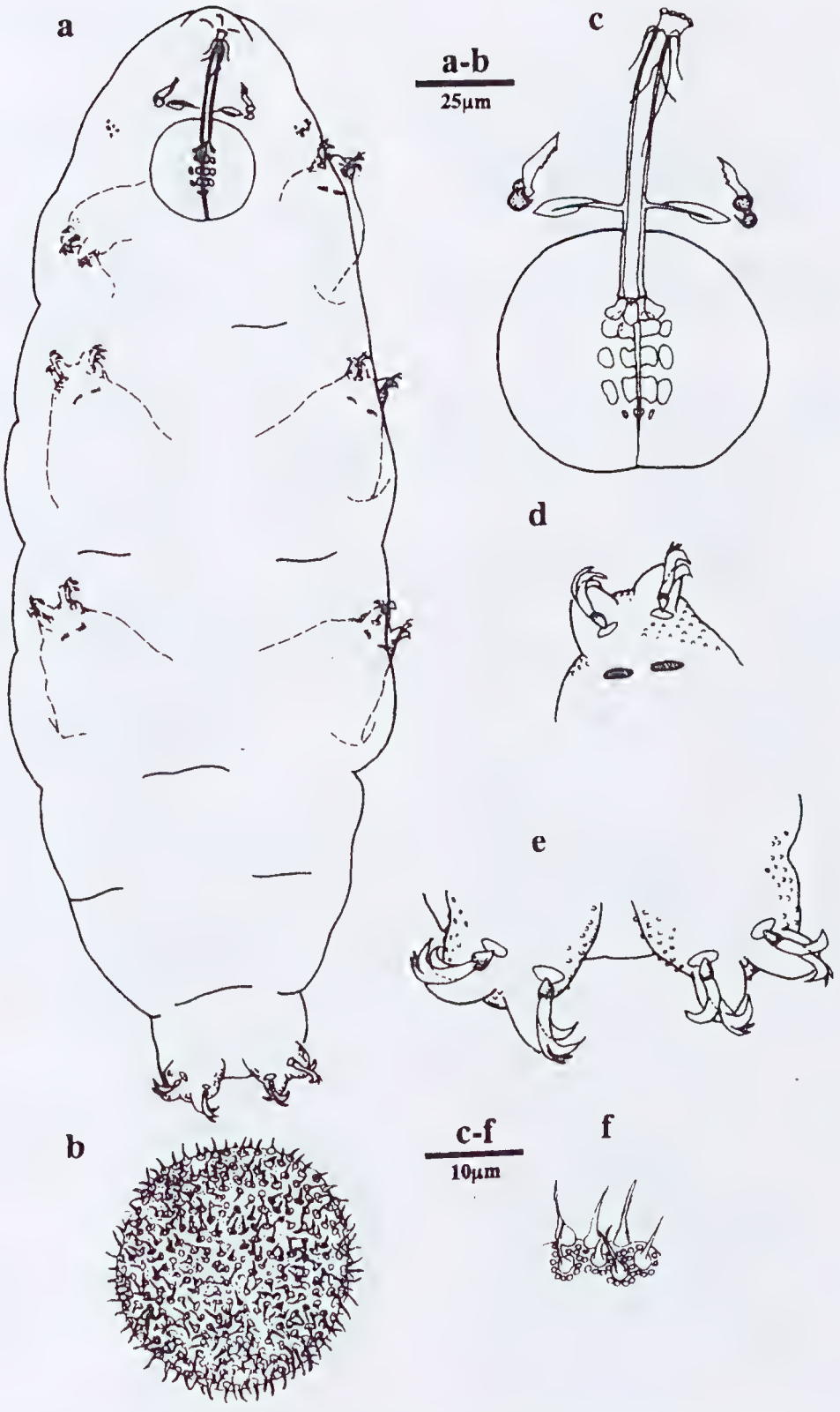

Figure 7. Taxonomic details of *Minibiotus hispidus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

the fourth pair of legs. It is perhaps most closely related to *Macrobiotus crassidens* Murray, 1907 (based on the somewhat inadequate description of that species) but differs from it by having eyes, by having a very indistinct microplacoid and by having egg processes that are narrower at the base, shorter and not touching.

Habitat. At the type locality the species was found in mosses and lichens on rocks and fallen logs in open woodland. At other Australian localities it was found in moss and lichen on rocks in open woodland but also can be found in leaf litter and sandy soil. The species can cope with high temperatures and drying.

Minibiotus pilatus n.sp.

Figs. 8, 17b, 19a; Table 7

Type material. HOLOTYPE in AM (AM KS41478): Australia, New South Wales: Cambewarra Mountain, 34°48'S 150°35'E, 625 m a.s.l., 9 May 1993, S.K. Claxton. PARATYPES (3 specimens, 2 eggs in AM [AM KS41479–KS41483]; 3 specimens, 2 eggs in SKC): same data as holotype.

Additional material examined. QUEENSLAND: Cunningham's Gap 28°03'S 152°25'E, 10 January 1996, S.K. Claxton, lichens on branches on ground in cool temperate rainforest, 8 specimens in SKC.

Diagnosis. Cuticle with a wrinkled pattern on the dorsum (Fig. 17b) and granulation on all legs; 3 small round macroplacoids and an indistinct microplacoid; robust claws with long, low accessory claws and lightly toothed lunules on the fourth pair of claws.

Description. Body length 150–290 µm, colourless. Eye spots with small, sparse dots, posterior. Cuticle with wrinkled pattern in transverse rows on the dorsum, granulation in a patch on outside of first three pairs of legs just above the external claw, also on back and sides of fourth pair of legs. Buccal tube narrow (7.9% of buccal tube length). Stylet supports inserted at 67.9% of buccal tube length and ventral support at 48.1%. Pharyngeal bulb round (about 28 µm diameter) containing large, round apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (30.4% of buccal tube length); first macroplacoid round and granular and slightly elongated anteriorly where it is partly obscured by the apophysis; second macroplacoid granular and smaller than the others; third macroplacoid granular but with a caudal bulb which curves in towards the midline. Microplacoid very small, indistinct and close to third macroplacoid. Claws robust (fourth pair of claws is 29.7% of length of buccal tube) with long secondary branch and a round refractive base; accessory claws long and well developed close to main branch. Lunules on claws of first three pairs of legs small and smooth; on fourth pair of legs with a few small teeth.

Eggs colourless, round, diameter without processes 54 µm, with processes 68 µm. Fifty-six processes around circumference. Processes of two types; first javelin-shaped (Fig. 19a), height 5.5–8 µm, base 1–1.6 µm joined by a membrane where they are expanded in the middle. Second type of process a short rod, about 2 µm high. Javelin-shaped processes form circles about 10 µm diameter on the egg surface, short rods are scattered within the circles. Short rods appear to rise to surface of the membrane but do not protrude through as do the javelin-shaped processes.

Etymology. Latin, *pilatus*, armed with a javelin, which describes the egg, and in addition the species is dedicated to Dr G. Pilato in appreciation of his assistance.

Remarks. The species is very similar to other species of *Minibiotus* with three macroplacoids and granulation around the claws but differs from them by the transverse bands of sculpture on the cuticle, which is only visible at high magnification and by the distinctive egg.

Table 7. Measurements (in µm) of adults of *Minibiotus pilatus* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	7	150–290	234.7	53.2	20.1	264
BT length	7	20.0–28.1	25.0	2.9	1.1	26.0
BT width	7	1.4–2.2	2.0	0.3	0.1	2.1
SI length	7	13.5–19.2	17.0	2.0	0.8	17.6
VS length	7	9.7–13.5	12.0	1.3	0.5	12.4
PR length	7	5.4–10.8	8.8	1.8	0.7	9.7
MPR length	7	4.9–9.2	7.7	1.4	0.5	8.1
m1	7	1.1–3.2	2.5	0.7	0.3	2.7
m2	7	1.0–2.4	2.0	0.5	0.2	2.2
m3	7	1.1–2.7	2.3	0.6	0.2	2.7
microplacoid	7	0.5–1.1	0.8	0.3	0.1	1.1
PH length	7	18.0–29.0	24.7	4.0	1.5	27.0
PH width	7	18.0–30.0	25.4	4.5	1.7	30.0
claw I	7	5.1–7.0	6.3	0.7	0.3	6.5
claw II–III	7	5.7–7.6	6.9	0.7	0.3	7.0
claw IV	7	6.2–8.1	7.4	0.7	0.3	7.6

Habitat. The species was found in temperate rainforest at both localities; in foliose lichens on rock at the type locality and in foliose lichens on tree branches at Cunningham's Gap.

Minibiotus ethelae n.sp.

Figs. 9, 19b; Table 8

Type material. HOLOTYPE in AM (AM KS41484): Australia, New South Wales: Cobbitty, 34°01'S 150°40'E, 90 m a.s.l., 20 March 1994, E.S. Siebels. PARATYPES: same data as holotype but collected on 8 November 1985, 11 May 1991, 29 August 1992 and 20 March 1994, 7 specimens, 3 eggs in AM (AM KS41485–KS41494); 50 specimens, 19 eggs in SKC; 1 specimen, 1 egg in collection of Binda and Pilato (UCI).

Additional material examined. SOUTH AFRICA: Lydenberg, Transvaal, 2250 m, 6 May 1988, M. Filmer, lichens, 11

Table 8. Measurements (in µm) of adults of *Minibiotus ethelae* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	8	311–412	362.9	34.4	12.2	368
BT length	8	33.0–35.7	34.7	1.0	0.3	34.1
BT width	8	2.6–2.7	2.7	0.04	0.01	2.7
SI length	8	21.1–23.5	22.5	1.0	0.4	21.6
VS length	7	17.8–18.9	18.0	0.4	0.2	17.8
PR length	8	11.9–13.5	12.8	0.5	0.2	12.4
MPR length	8	10.3–11.4	11.2	0.4	0.2	10.8
m1	8	3.2–3.8	3.5	0.3	0.09	3.2
m2	8	2.4–2.7	2.7	0.1	0.04	2.7
m3	8	2.7–3.2	3.1	0.2	0.06	3.2
microplacoid	8	0.5–1.1	0.9	0.3	0.09	0.7
PH length	8	31.0–35.0	33.1	1.6	0.6	32.0
PH width	8	30.0–35.0	34.1	1.7	0.6	35.0
claw I	8	10.8–11.9	11.4	0.5	0.2	11.4
claw II–III	8	11.4–12.4	12.0	0.4	0.2	11.9
claw IV	8	12.4–13.5	13.0	0.5	0.2	13.0

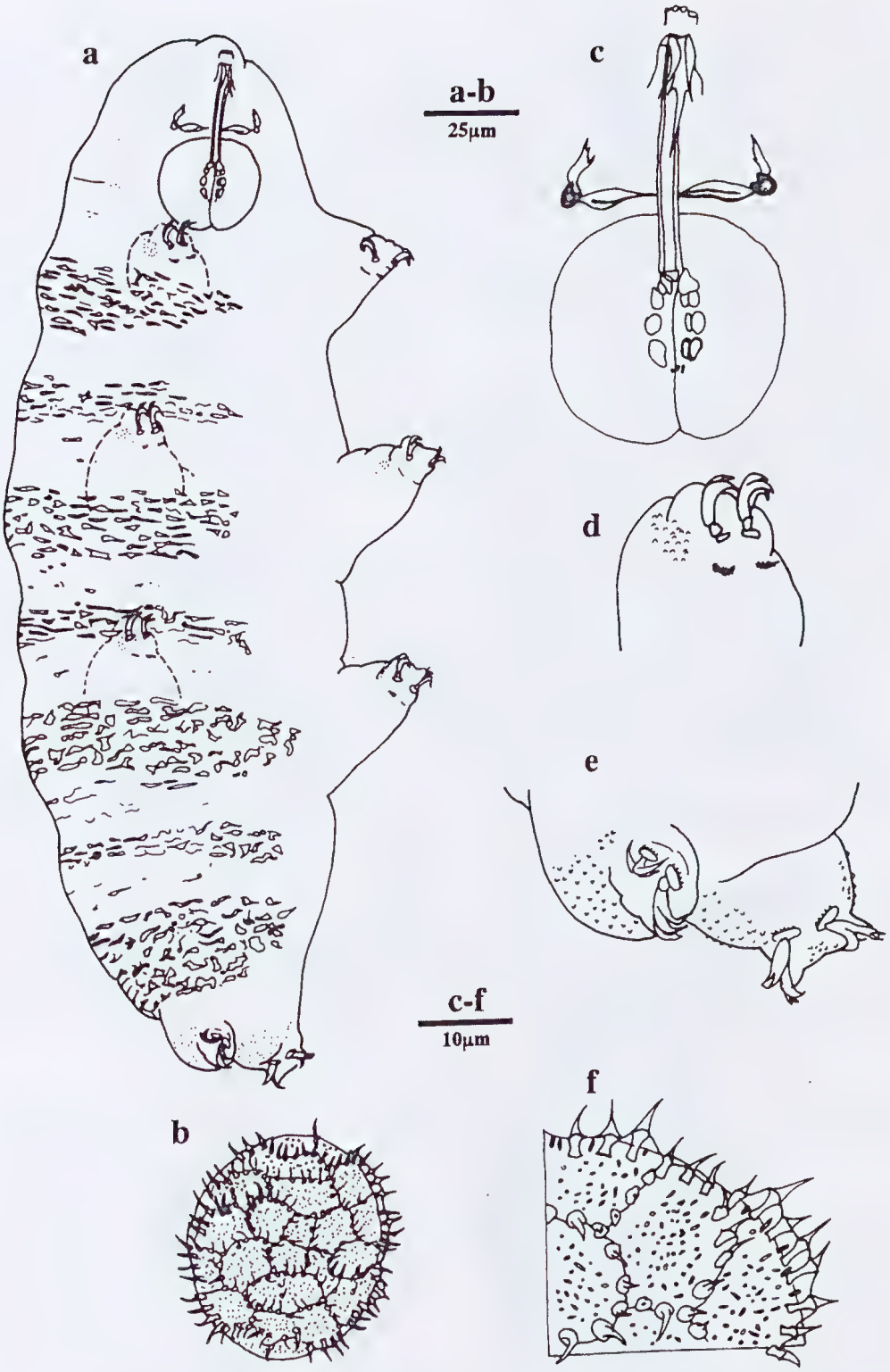

Figure 8. Taxonomic details of *Minibiotus pilatus* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

specimens, 2 eggs in NMP. Natal, Drakensberg, Cathedral Rock Area, 30 May 1988, H. Dastych, moss on rock in Indumeni forest, 4 specimens in NMP. Rus-Te-Winter National Reserve, 1500 m, 30 May 1988, M. Filmer, bark of *Acacia*, 2 specimens (NMP). Kruger National Park, 20 May 1988, S. Neses, lichens on dead twigs, 8 specimens in ZIM. Hendriksdaal, Palmers Creek, 1400 m, July 1971, A. Szeptycki, rock, 1 specimen in ZIM.

Diagnosis. Pale yellow body cells and variably shaped pores in the cuticle, cuticle thickened in caudal region; 3 small round macroplacoids and an indistinct microplacoid; long, slender claws with low accessory claws and smooth lunules.

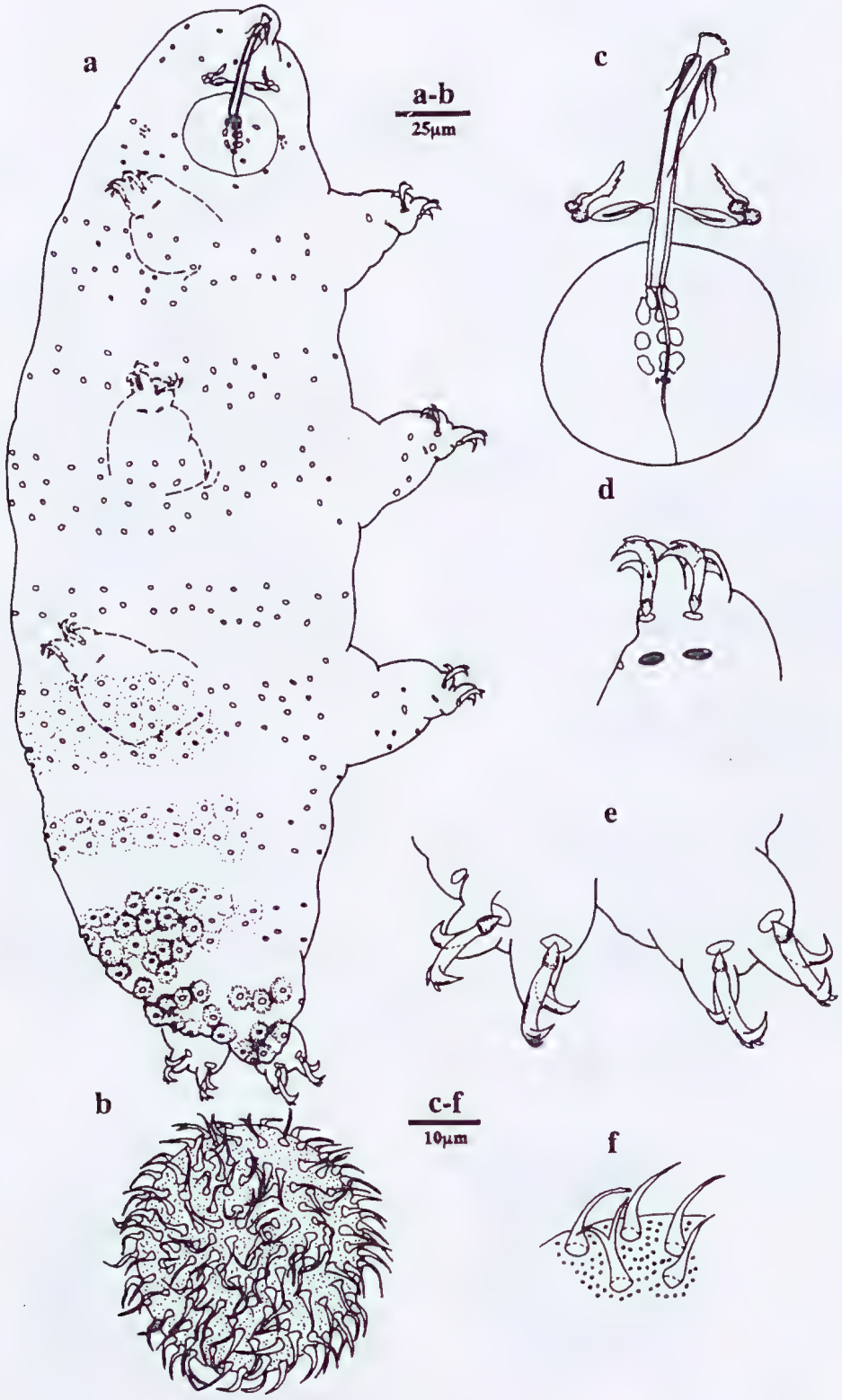

Figure 9. Taxonomic details of *Minibiotus ethelae* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Description. Body length 175–480 µm, yellow body cells. Large, posterior eye spots present. Cuticle with nine transverse bands of large pores (round, elliptical, trifoliate and quadrifoliate) around the body; pores also on the legs. Cuticle thickened in the caudal region. Buccal tube narrow (7.6% of buccal tube length). Stylet supports inserted at 64.9% of buccal tube length and ventral support 51.4%. Pharyngeal bulb round (about 32 µm diameter) containing large round apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.3% of buccal tube length); first macroplacoid pear-shaped and partly obscured by apophysis, second

granular and smaller than the other two and third granular with caudal bulb that curves towards midline. Microplacoid small, indistinct and lies very close to third macroplacoid. Claws slender (fourth pair of claws is 37.6% of length of buccal tube) with small but obvious refractive zone at base and long secondary branch; short but well developed accessory claws lie close to main branch. Lunules small, smooth and thin on all claws.

Eggs colourless, round, diameter without processes 67–70 µm, with processes 90–100 µm. 28–34 processes around circumference and 120–160 in hemisphere. Processes are cones tapering rapidly to attenuated tip, often bifurcate. Process height variable, on one egg 12–14 µm, on three others 14.5–19 µm and on another 19–22.5 µm. Base diameter of processes 2.7–3.8 µm (on egg with longest processes 4.3–4.9 µm), about 5 µm apart. Shell surface dotted, SEM shows these to be bumps (Fig. 19b).

Etymology. The species is named after Ethel Siebels who kindly assisted in the collection of the specimens.

Remarks. The species is similar to *Minibiotus furcatus* but differs from it by having the stylet supports inserted more anteriorly, by having a much shorter ventral support and shorter placoids, by having smooth lunules on all legs and having much longer egg processes and a dotted shell. It differs from *Minibiotus ramazzottii* Binda & Pilato, 1992 by having large showy pores in the cuticle and from *Minibiotus vinciguerrae* Binda & Pilato, 1992 by having no granulation around the claws and longer, thinner egg processes.

Habitat. At the type locality the species was found in crustose and foliose lichens on the trunk of a *Casuarina* tree and a peppercorn tree in a suburban street.

Minibiotus keppelensis n.sp.

Figs. 10, 19c; Table 9

Type material. HOLOTYPE in AM (AM KS41495): Australia, Queensland: Great Keppel Island, 23°10'S 150°59'E, 14 July 1993, P.D. Claxton. PARATYPES (4 specimens, 2 eggs in AM [AM KS41496–KS41501]; 13 specimens, 4 eggs in SKC) same data as holotype.

Diagnosis. Cuticle smooth with 10 transverse rows of round pores and granulation on all legs; 3 small round macroplacoids and an indistinct microplacoid; robust claws with long, low accessory claws and smooth lunules.

Description. Body length 180–287 µm, colourless, some specimens with red pigment granules. Eye spots large, in posterior position. Cuticle smooth with round (1 µm) pores arranged in ten distinct transverse bands around body and on legs. Fine granulation on top and both sides of claws on first three pairs of legs and on back and sides of fourth pair of legs. Buccal tube very narrow (5.8% of buccal tube length). Stylet supports inserted at 60.6% of the buccal tube length, ventral support short (40.4% of buccal tube length). Pharyngeal bulb oval to round (27×30 µm), placoids in anterior half; containing three macroplacoids and a microplacoid. Macroplacoid row short (26.6% of buccal tube length); macroplacoids small, granular as are apophyses which are about the same size as the first macroplacoid. First macroplacoid round, slightly elongated anteriorly where it lies beneath the apophysis; second macroplacoid granular smaller than other two; third macroplacoid granular but with slight caudal bulb which curves towards midline. Microplacoid small, indistinct and lies very close to third macroplacoid. Claws robust (fourth pair of claws is 30.1% of buccal tube length) with large refractive zone at base and with long secondary branch; long accessory claws lie close to main branch on all claws. Lunules small, smooth on all claws.

Eggs colourless, round, diameter without processes 45–55 µm, with processes 65–85 µm. Eleven processes around circumference and 24 in hemisphere. Processes short cones with pointed apices 11–16 µm high, base diameter 9–12 µm and 4–6 µm apart. Base of each process surrounded by about ten pores. Membrane around each process reaching half way up the side and apparently supported in between processes by struts (4 µm high) so that the shell surface appears dotted.

Etymology. The species is named after the type locality, Great Keppel Island.

Remarks. The egg processes of this species are very similar to those of *M. macularta* but the adult differs from that species by having rows of large pores around the body.

Habitat. The species was found in foliose lichen on rock and in crustose lichen on a dead tree in open woodland.

Table 9. Measurements (in µm) of adults of *Minibiotus keppelensis* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	12	200–287	259.4	25.4	7.3	270
BT length	12	24.9–28.4	26.9	1.2	0.3	27.0
BT width	12	1.4–1.7	1.6	0.08	0.02	1.5
SI length	12	15.1–17.3	16.3	0.8	0.2	16.2
VS length	12	9.7–11.9	10.9	0.7	0.2	10.8
PR length	12	7.6–8.7	8.1	0.4	0.1	8.1
MPR length	12	7.0–7.6	7.2	0.2	0.07	7.0
m1	12	1.6–2.7	2.2	0.3	0.08	2.2
m2	12	1.6–2.2	1.8	0.2	0.06	1.9
m3	12	1.6–2.2	2.0	0.3	0.08	2.2
microplacoid	12	0.5–0.8	0.6	0.1	0.03	0.5
PH length	11	24.0–30.0	26.7	2.2	0.7	27.0
PH width	11	23.0–31.0	27.6	2.9	0.9	30.0
claw I	12	6.0–7.0	6.7	0.4	0.1	7.0
claw II–III	12	6.5–7.6	7.3	0.4	0.1	7.6
claw IV	12	7.0–8.6	8.1	0.6	0.2	8.6

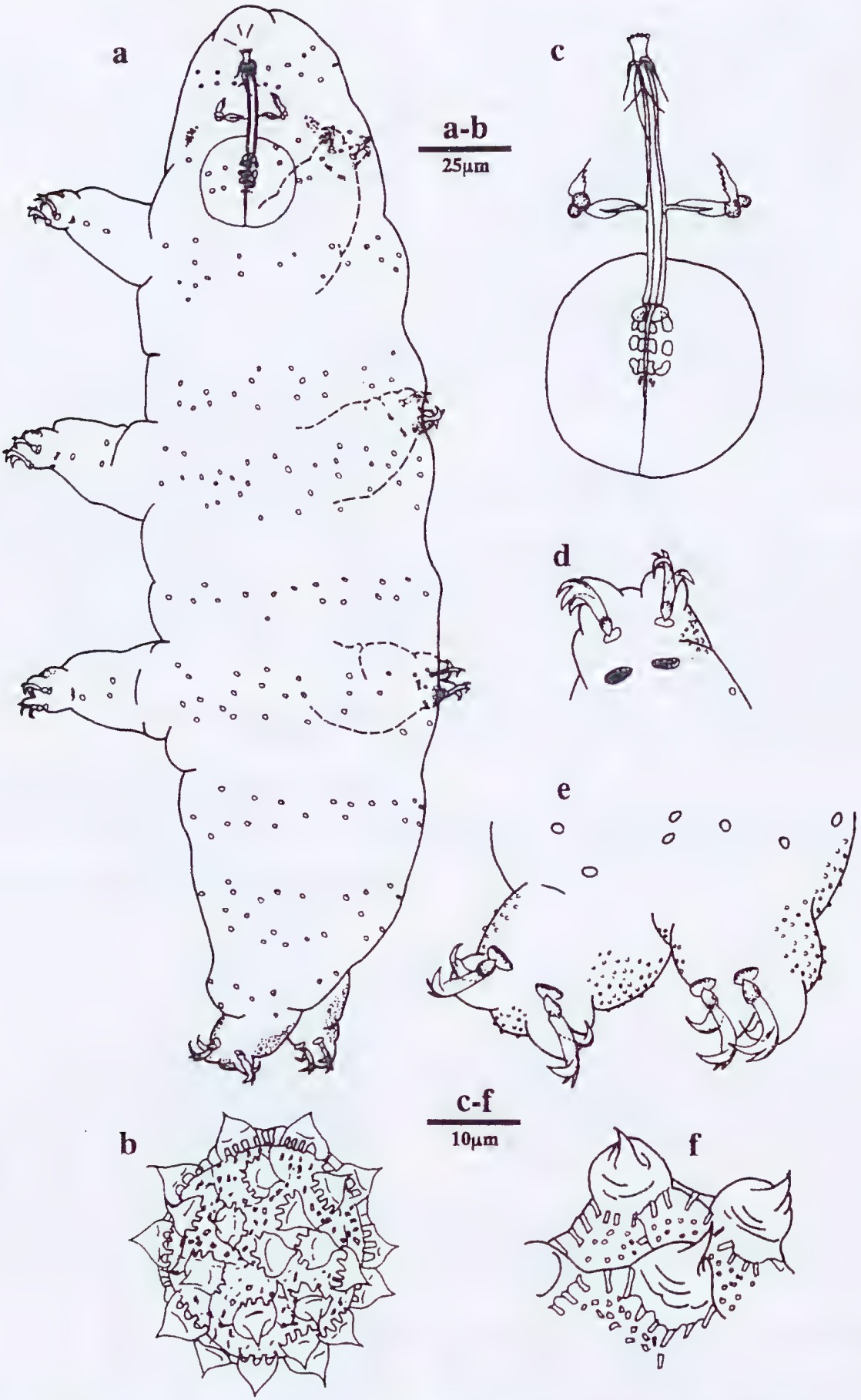

Figure 10. Taxonomic details of *Minibiotus keppelensis* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Minibiotus asteris n.sp.

Figs. 11, 19d; Table 10

Type material. HOLOTYPE in AM (AM KS41502): Australia, Tasmania: O'Neill's Creek, Mount Roland Protected Area, 41°29'S 146°15'E, 680 m a.s.l., 21 May 1996, A. Moscal. PARATYPES (5 specimens, 3 eggs in AM [AM KS41503–KS41510]; 80 specimens, 17 eggs in SKC) same data as holotype.

Additional material examined. AUSTRALIA TASMANIA: Mount Montgomery 41°09'S 146°47'E, 470 m, 20 October 1994, A. Moscal, moss on rock in low woodland, 11 specimens in SKC. Hartz Mountains, 43°25'S 146°47'E, 4 December 1988, A.J. Downing, moss on mudstone in *Eucalyptus*/Myrtle forest, 6 specimens, 3 eggs in SKC. VICTORIA: Melba Gully, Otway Ranges, 38°40'S 143°20'E, 4 May 1997, S.K. Claxton, leafy liverwort, moss and lichen on fallen branches in *Nothofagus* forest, 33 specimens, 2 eggs (SKC). MACQUARIE ISLAND: Scobie Lake, 400 m, 9 December 1977, D.S. Horning, 26 specimens. Gadget's Gully, 220 m, 25 November 1977, D.S.H., 17 specimens. Lusitania Bay, 400 m, 1 December 1977, D.S.H., 7 specimens. Mount Hamilton summit, 433 m, 17 January 1978, D.S.H., 8 specimens. Mount Waite summit, 452 m, 29 December 1977, D.S.H., 11 specimens. Mount Fletcher summit, 428 m, 17 February 1978, D.S.H., 8 specimens. All Macquarie Island specimens in WM. NEW ZEALAND, SOUTH ISLAND: Temple Basin Lower Ski Huts, Arthur's Pass National Park, 19 May 1970, D.S. Horning, 2 specimens (NZ186, 188). Pegley Flat, Arthur's Pass National Park, 18 May 1970, D.S.H., 1 specimen (NZ170). Fox Glacier Valley, 28 March 1970, D.S.H., 3 specimens (NZ23) in NZM.

Diagnosis. Cuticle smooth with irregularly shaped pores over the whole cuticle and granulation on fourth pair of legs only; 3 small round macroplacoids and a distinct microplacoid; short, robust claws with high accessory claws and smooth lunules.

Description. Body length 128–361 µm, colourless. Eye spots in posterior position. Cuticle over the whole body is covered with small round (0.5–0.7 µm) pores; larger pores (about 2 µm) with irregular shape rare but more common towards the rump. Fine granulation around claws on fourth pair of legs only. Buccal tube narrow (8% of buccal tube length). Stylet supports inserted at 63.8% of buccal tube length, ventral support short (44.8% of length of buccal tube). Pharyngeal bulb round (26 µm diameter) containing well-developed granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (30% of buccal tube length); macroplacoids equal in size; first macroplacoid granular, lying close to apophysis and partly obscured by it; second macroplacoid granular as is third which has a slight bulb at the caudal end that curves towards the midline. Microplacoid short, distinct and lies close to third macroplacoid. Claws robust (fourth pair of claws is 28% of buccal tube length) with small refractive zone at base and long secondary branch; accessory claws short and rising well clear of main branch. Lunules small and smooth on all claws.

Eggs colourless, round, diameter without processes 54–67 µm, with processes 64–85 µm. 20–28 processes around circumference, 75–90 in a hemisphere. Processes like those of *Macrobiotus hufelandi* but with distal disk consisting of about six (up to eight) distinct arms like those of a starfish. Process height 5–10 µm, base diameter 4.3–7.0 µm and disk diameter 4.3–5.4 µm. Processes are 2–4 µm apart. 12–14 small pores around the base of each process. Egg shell surface smooth or lightly striated.

Table 10. Measurements (in µm) of adults of *Minibiotus asteris* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	20	155–368	259.7	62.8	14.0	274
BT length	20	21.6–30.8	26.7	3.0	0.7	28.1
BT width	20	1.6–2.8	2.1	0.3	0.07	2.2
SI length	20	13.5–19.5	17.0	2.0	0.5	18.1
VS length	20	9.7–14.1	12.0	1.4	0.3	12.4
PR length	20	7.0–11.9	9.4	1.4	0.3	9.2
MPR length	20	6.0–10.3	8.0	1.2	0.3	8.1
m1	20	1.6–3.2	2.4	0.5	0.1	2.4
m2	20	1.6–2.7	2.2	0.4	0.09	2.4
m3	20	1.6–2.7	2.2	0.4	0.09	2.4
microplacoid	20	0.7–1.4	1.1	0.2	0.04	0.8
PH length	20	22.0–33.0	26.7	3.5	0.8	27.0
PH width	20	22.0–36.0	26.5	3.6	0.8	27.0
claw I	20	4.9–7.6	6.3	0.9	0.2	7.0
claw II–III	20	5.4–8.2	6.9	0.9	0.2	7.6
claw IV	20	6.0–8.9	7.5	1.0	0.2	8.1

Etymology. Latin *aster* with masculine ending *is*, star, describes the appearance of the distal end of the egg processes.

Remarks. This species is probably most closely related to *Macrobiotus allani* Murray, 1913 as far as is possible to tell from the original description. It differs from that species by having eyes, pores in the cuticle, a strong microplacoid and by the nature and number of disk arms on the egg processes.

Habitat. At the type locality the species was found in mosses and liverworts on soil and rocks on a northwest gully slope in a wet *Eucalyptus delegatensis* forest.

Minibiotus milleri n.sp.

Figs. 12, 16b, 19e; Table 11

Type material. HOLOTYPE in AM (AM KS41599): Australia, New South Wales: New England National Park, 30°30'S 152°24'E, 1450 m a.s.l., 18 December 1994, S.K. Claxton. PARATYPES (7 specimens, 4 eggs in AM [AM KS41600–KS41608]; 56 specimens, 4 eggs in SKC) same data as holotype but some also collected on 20 April 1995 and 7 January 1996.

Additional material examined. NEW SOUTH WALES: Cambewarra Mountain, 34°48'S 150°35'E, 625 m, 9 May 1993, S.K. Claxton, moss and lichen on rocks and trees in cool temperate rainforest, 14 specimens in SKC.

Figure 11. Taxonomic details of *Minibiotus asteris* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Diagnosis. Smooth cuticle with fine granulation near claws, long bean-shaped macroplacoids and a distinct microplacoid; robust claws with short, high accessory claws and smooth lunules.

Description. Body length 149–398 µm, colourless. Eye spots in the posterior position consisting of large granules. Cuticle smooth, fine granulation around claws on all legs. Oral cavity long with single tooth ventrally just above stylet sheaths in some larger specimens. Buccal tube narrow (*pt* 9.7); stylet supports inserted at 73% of buccal tube length; ventral support very short (*pt* 36.4). Pharynx round (27 µm diameter) containing small apophyses, three macroplacoids and a microplacoid. Macroplacoid row long (37%

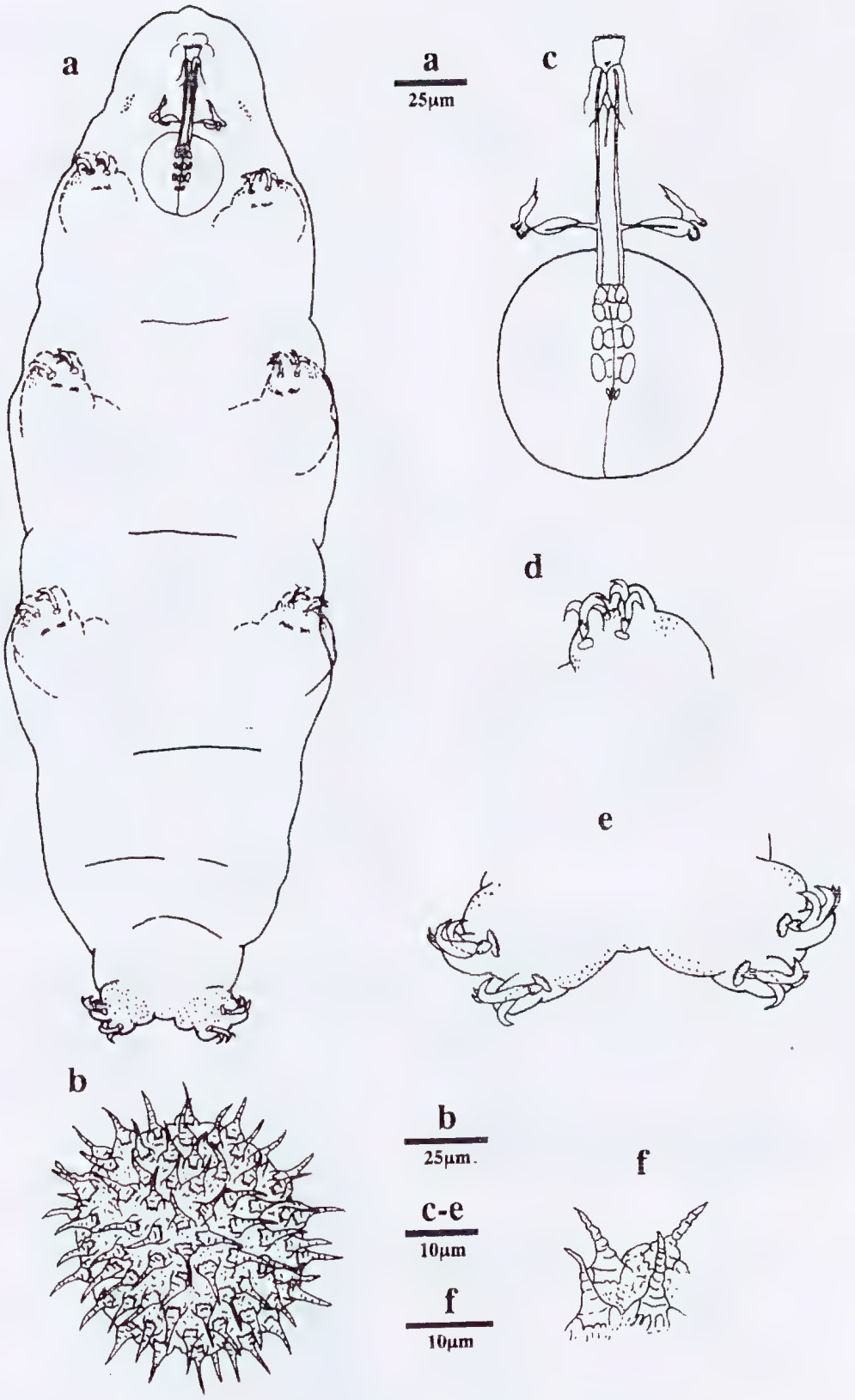

Figure 12. Taxonomic details of *Minibiotus milleri* n.sp. **a**, habitus (holotype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

of buccal tube length); first macroplacoid smallest, somewhat pear-shaped, lying close to apophysis and partly obscured by it; second granular, slightly longer than first; third longest. Microplacoid long, distinct, lying close to third macroplacoid. Claws robust (fourth pair of claws is 26.5% of buccal tube length) with long secondary branch, well divided. Round refractive zone at base of claws well developed. Accessory claws short, raised high above main branch. Lunules on first three pairs of legs very small, smooth; on fourth pair smooth.

Table 11. Measurements (in µm) of adults of *Minibiotus milleri* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	20	182–398	272.6	60.2	13.5	349
BT length	20	24.3–35.1	29.1	3.3	0.7	31.9
BT width	20	2.3–3.5	2.8	0.4	0.09	3.2
SI length	20	17.3–26.0	21.2	2.5	0.6	23.0
VS length	20	8.7–12.7	10.6	1.3	0.3	11.9
PR length	20	10.8–15.7	12.9	1.5	0.3	14.1
MPR length	20	8.7–13.0	10.8	1.3	0.3	11.4
m1	20	2.2–3.2	2.7	0.3	0.07	3.0
m2	20	2.4–3.5	2.9	0.3	0.07	3.2
m3	20	2.7–4.1	3.4	0.5	0.1	3.5
microplacoid	20	0.8–1.9	1.4	0.3	0.07	1.6
PH length	20	23.0–35.0	27.7	2.8	0.6	29.0
PH width	20	23.0–33.0	26.8	2.7	0.6	27.0
claw I	20	4.9–7.6	6.4	0.9	0.2	7.0
claw II–III	20	5.4–8.7	7.0	0.9	0.2	7.6
claw IV	20	6.5–9.7	7.7	1.0	0.2	8.7

Eggs round, diameter without processes 68–74 µm, with processes 90–98 µm. 20–30 processes around circumference, 80–120 in hemisphere. Processes long cones tapering to blunt tip, rarely bifurcate, lower part of each cone indented and enclosed in membrane. Tapering portion above with rough surface which appears as transverse lines. Process height 10–14 µm, base diameter 3 µm arranged evenly about 3 µm apart. Shell surface faintly striated.

Etymology. The species is named after Dr William R. Miller, friend and colleague.

Remarks. This species is similar to *M. hufelandioides* and *M. aquatilis* in having a long macroplacoid row, stylet supports inserted a long way down the buccal tube and no bend in the tube as it enters the pharynx but may be distinguished from these species by its very short ventral support.

Habitat. At the type locality, specimens were recovered from moss on rock, moss and lichen on tree trunks and branches in cool temperate rainforest and *Banksia collina* thickets.

Minibiotus hufelandioides (Murray, 1910) **n.comb.**

Figs. 1a, 13, 19f; Table 12

Macrobiotus hufelandioides Murray, 1910: 138–139, pl. XVIII, figs. 29a–c.

Material examined. Australia: NEW SOUTH WALES: Kosciusko (type locality), Digger's Creek, 36°20'S 148°30'E, 1500 m, 1 October 1992, P.D. Claxton, moss and lichen on rock in open alpine area, 58 specimens, 16 eggs. Thredbo Creek, 36°27'S 147°55'E, 1200 m, 1 October 1992, P.D.C., moss and lichen on rock in open alpine area, 10 specimens, 1 egg. Waste Point, 36°20'S 148°36'E, 1000 m, 1 October 1992, P.D.C., moss and lichen on rock, 4 specimens, 1 egg. Lake George, 35°04'S 149°23'E, 27 March 1992, P.D.C., moss and lichen on rock in open forest, 29 specimens, 24 eggs. Galore, 35°07'S 146°47'E, 340 m, 19 March 1994, S.K.C., moss and lichen on rocks on summit of monolith in open forest, 19 specimens, 1 egg. All SKC.

Diagnosis. Smooth cuticle with granulation on all legs; three long macroplacoids and an indistinct microplacoid; robust claws with long, high accessory claws and toothed lunules on fourth pair of claws.

Description. Body length 149–419 µm, colourless. Eyes large, posterior. Cuticle smooth except for strong granulation over back and outside of all legs around claws. Buccal tube narrow (8.6% of buccal tube length). Stylet supports inserted at 67.4% of buccal tube length, ventral support short (45.9% of buccal tube length). Pharynx round (30 µm diameter) containing large apophysis, three macroplacoids and a microplacoid. Macroplacoid row long (38.2% of buccal tube length); first macroplacoid pear-shaped and partly obscured by apophysis; second macroplacoid round, slightly shorter than other two; third macroplacoid kidney-shaped and about same size or slightly longer than the first. Microplacoid indistinct and lies close to third macroplacoid. Claws long and robust (fourth pair of claws is 29.3% of buccal tube length) with large, clear refractive base and short secondary branch. Accessory claws long and high above main branch. Lunules small and smooth on first three pair of legs, jagged or toothed on fourth pair.

Eggs colourless, round, diameter without processes 54–64 µm, with processes 65–75 µm. 20–26 processes around circumference. Processes conical with expanded discoid tops, distal disk smooth or lightly notched; process height 5.5–6.5 µm, base diameter 5.5–7 µm, disk diameter 4.5–6.5 µm. Each process with a ring of pores around the base; shell surface lightly granulated.

Remarks. The original type material was not located. The main repository of James Murray's permanent slides is the Royal Scottish Museum, Edinburgh (Morgan, 1977). No Australian tardigrades are represented in that collection.

Table 12. Measurements (in µm) of adults of *Minibiotus hufelandioides*.

Character	No.	Range	Mean	SD	SE
body length	16	240–378	315.2	43.0	10.8
BT length	16	24.9–34.6	28.9	2.6	0.7
BT width	16	2.0–3.1	2.5	0.3	0.08
SI length	16	16.8–23.7	19.5	1.8	0.5
VS length	16	10.8–16.2	13.3	1.5	0.4
PR length	16	10.8–16.2	13.0	1.4	0.4
MPR length	16	9.2–13.5	11.0	1.1	0.3
m1	16	2.7–3.5	3.0	0.3	0.07
m2	16	2.2–3.0	2.6	0.2	0.06
m3	16	2.7–3.8	3.1	0.4	0.09
microplacoid	16	0.8–1.6	1.2	0.3	0.08
PH length	16	28.0–41.0	32.1	3.4	0.9
PH width	16	26.0–42.0	32.3	4.7	1.2
claw I	16	6.0–8.7	7.3	0.8	0.2
claw II–III	16	6.5–9.2	7.8	0.8	0.2
claw IV	16	7.0–9.7	8.5	0.9	0.2

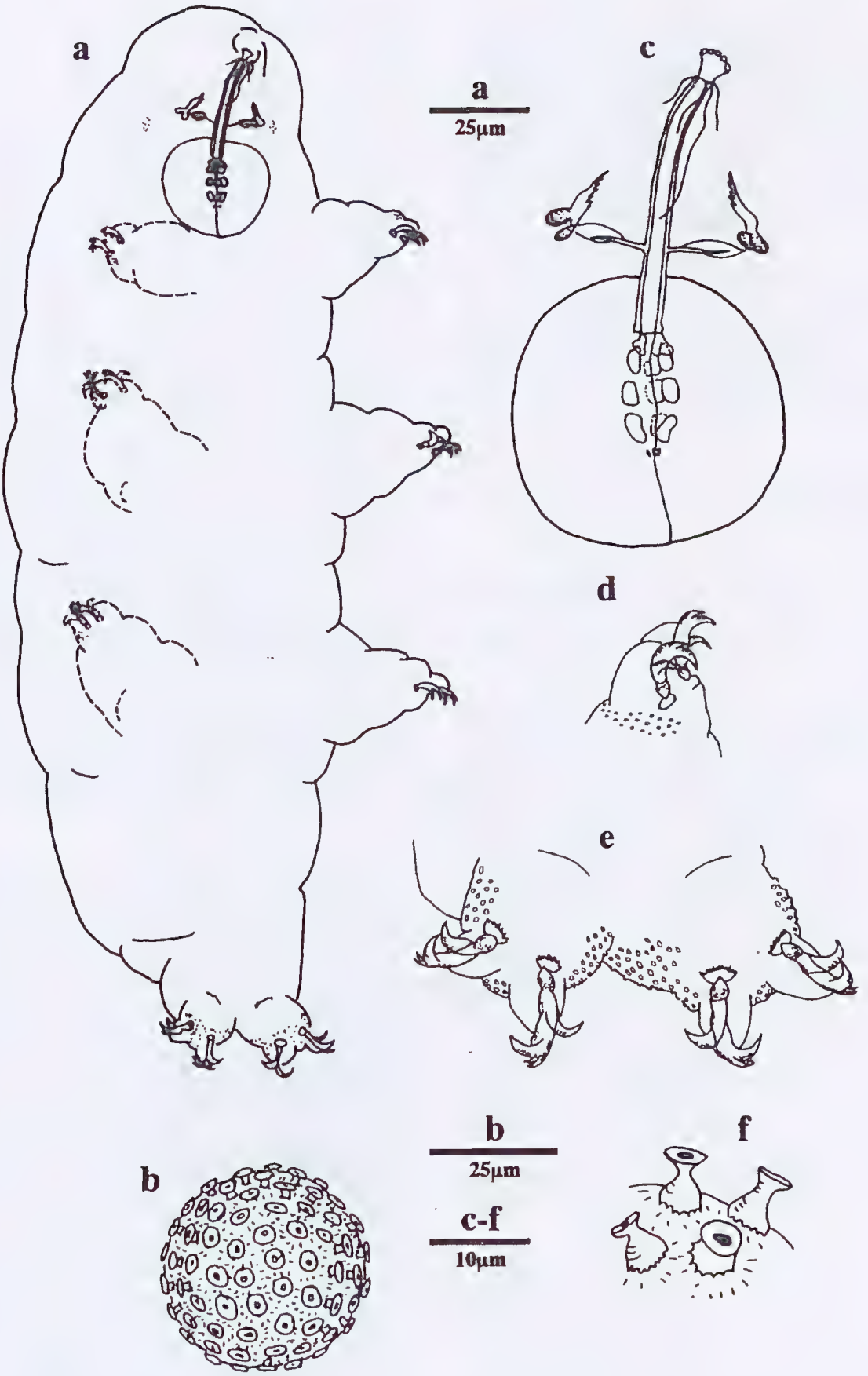

Figure 13. Taxonomic details of *Minibiotus hufelandioides* **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Although Murray's description lacks detail such as the granulation around the claws and the toothed lunule on the fourth pair of legs, the identification of these specimens and eggs is not in doubt. His description of the animal having "three rods in the pharynx of nearly equal size,... no comma or a very small and obscure one,... eggs with processes like those of the typical *hufelandi* egg,... processes taper from a broad base which is surrounded by a circlet of dots..." agrees with the specimens described here.

Habitat. Murray (1910) indicated that the species was found in mosses at the Hospice on Mount Kosciusko. The material obtained for this study was found in mosses, fruticose and foliose lichens on rocks at the site of the Hospice (Digger's Creek). This species was the most abundant of the 31 species collected at Kosciusko in October 1992.

Minibiotus aculeatus (Murray, 1910) **n.comb.**

Figs. 1b, 14, 16a, 17a, 20a; Table 13

Macrobiotus aculeatus Murray, 1910: 139–140, pl. XVIII, figs. 27a–e.

Macrobiotus intermedius subjulietae Horning, Schuster & Grigarick, 1978: 237, figs. 117–120.

Material examined. AUSTRALIA: NEW SOUTH WALES: Kosciusko (type locality), Digger's Creek, 36°20'S 148°30'E, 1500 m, 1 October 1992, P.D. Claxton, moss on rock, 1 specimen. Thredbo Creek, 36°27'S 147°55'E, 1200 m, 1 October 1992, P.D.C., lichen on rock, 7 specimens, 1 egg. Waste Point, 36°20'S 148°36'E, 1000 m, 1 October 1992, P.D.C., lichen on rock, 1 egg. New England National Park, 30°30'S 152°30'E, 1400 m, 18 December 1994, S.K. Claxton, moss and lichen on rocks and trees in *Banksia* heath, 36 specimens, 2 eggs; *ditto* but collected 20 April 1995, S.K.C., moss and lichen on rock in heath, 13 specimens, 1 egg; *ditto* but collected on lichen on tree in *Nothofagus* forest, 1 specimen; *ditto* but collected 7 January 1996, S.K.C., moss and lichen in heath, 91 specimens, 4 eggs. Jenolan, 33°49'S 150°02'E, 14 December 1986, S.K.C., moss on trees and rocks in sheltered valley, 22 specimens, 6 eggs. Barrington Tops, 31°59'S. 151°30'E, 8 February 1993, D. Clark, moss on branch on ground in closed forest, 1 specimen. Mount Wilson, 33°30'S 150°23'E, 27 October 1991, S.K.C., moss on tree in cool temperate rainforest, 1 specimen, 1 egg. QUEENSLAND: Ravensbourne, 27°22'S 152°08'E, 3 September 1985, S.K.C., moss on tree in closed forest, 5 specimens. LORD HOWE ISLAND, D.S. Horning, 6 specimens. TASMANIA: Mount Pedder, Maria Island National Park, 42°38'S 148°05'E, 620 m, 20 April 1995, A. Moscal, moss on rock in heath, 7 specimens. All SKC.

NEW ZEALAND: 16 paratypes of *Macrobiotus intermedius subjulietae*: NORTH ISLAND: Waimaua Gorge, 17 May 1971, C.J. Horning, 1 specimen (NZ650). Grays Bush, 19 May 1971, C.J.H., 1 specimen (NZ672). Bruce Park Scenic Reserve, 21 May 1971, D.S. Horning, 3 specimens (NZ705). Taumarunui, 15 July 1970, B.J. Donovan, 2 specimens (NZ279, NZ281). Norsewood, 20 May 1971, D.S.H., 1 specimen (NZ687). Mount Egmont National Park, 23 May 1971, D.S.H., 1 specimen (NZ753). Morere Hot Spring Scenic Reserve, 19 May 1971, D.S.H., 1 specimen (NZ674). SOUTH ISLAND: Abel Tasman National Park, 9 April 1971, D.S.H., 1 specimen (NZ538). Cowper's Knob, 9 April 1970, D.S.H., 1 specimen (NZ86). West Harper Hut, 12 April 1971, H.A. Best, 1 specimen (NZ544). CHATHAM ISLAND: Waterfall Creek, 31 August 1971, D.S.H., 2 specimens (NZ932, NZ924). THREE KINGS ISLAND: Summit Ridge, 28 November 1970, G.W. Ramsey, 1 specimen (NZ479). All NZM

Table 13. Measurements (in µm) of adults of *Minibiotus aculeatus*.

Character	No.	Range	Mean	SD	SE
body length	7	210–350	290.6	43.8	16.6
BT length	7	24.9–32.4	29.1	2.5	1.0
BT width	7	1.9–2.5	2.3	0.2	0.08
SI length	7	15.7–20.8	18.5	1.7	0.7
VS length	7	13.0–16.8	15.0	1.4	0.5
PR length	7	9.7–12.2	11.1	0.9	0.4
MPR length	7	7.3–10.5	9.4	1.1	0.4
m1	7	2.2–3.2	2.8	0.4	0.1
m2	7	1.6–2.7	2.3	0.4	0.1
m3	7	1.6–3.0	2.4	0.5	0.2
microplacoid	7	0.6–1.1	1.0	0.2	0.08
PH length	7	27.0–34.0	29.6	2.7	1.0
PH width	7	27.0–38.0	31.1	3.4	1.3
claw I	7	4.3–6.0	5.6	0.6	0.2
claw II–III	7	4.7–6.5	6.1	0.7	0.3
claw IV	7	5.4–7.0	6.6	0.6	0.2

Diagnosis. Smooth cuticle with pores of variable size and shape and three pairs of soft spines (Fig. 17a) over legs II, III and IV (or one pair over leg IV); three small round macroplacoids and a distinct microplacoid; short, robust claws with prominent accessory claws and very small refractive base and lunules.

Description. Body length 204–350 µm most specimens pink or pale brown in colour. Eyes in the posterior position. Cuticle covered with small (0.5 µm diameter) round pores and, more sparsely, large triangular or star-shaped pores; large pores often with thickened rims. A ring of about ten pores around the mouth below the sensory fields are visible only under the highest light magnification and appear as slits in specimens prepared for SEM (Fig. 1b). The shape under SEM is probably due to distortion of the specimen during preparation. Three pairs of soft, conical spines (about 7 µm long) on body, one pair each above the last three pairs of legs. No teeth in oral cavity, buccal tube narrow 2 µm (*pt* 7.8). Stylet supports inserted at 63.7% of length of buccal tube, ventral reinforcing bar 51.4% of buccal tube length. Pharyngeal bulb oval (27×30 µm) containing well developed, granular apophyses, three macroplacoids and a microplacoid. Macroplacoid row short (32.2% of buccal tube length); first macroplacoid pear-shaped lying close to apophysis and partly obscured by it, second and third macroplacoids granular and similar in size. Microplacoid small, distinct and lies close to third macroplacoid. Claws short, robust (fourth pair of claws is 22.8% of buccal tube length) with no refractive zone at the base; accessory claws long and rising well clear of main branch. Lunules very small.

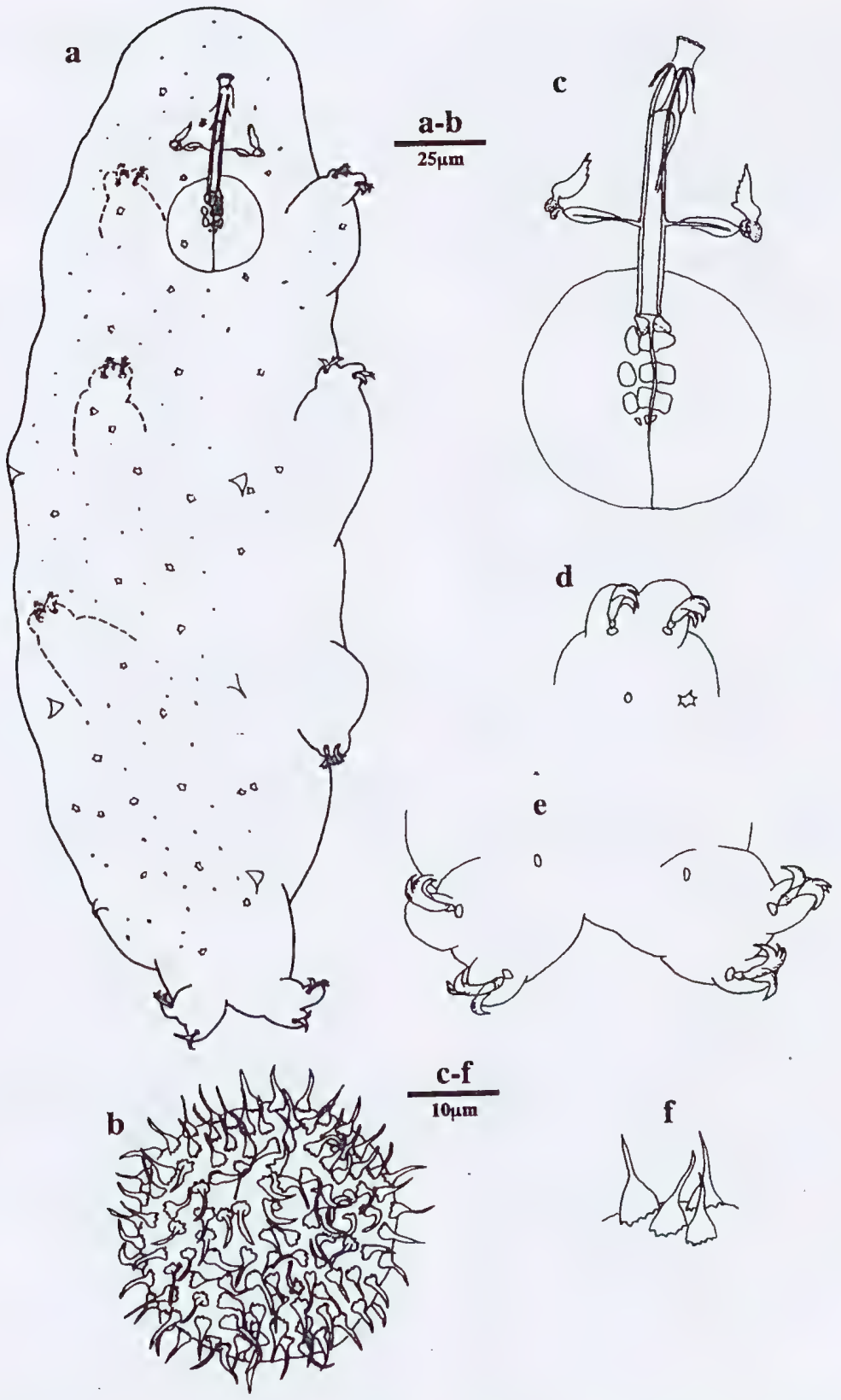

Figure 14. Taxonomic details of *Minibiotus aculeatus* **a**, habitus; **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

Eggs colourless, round, diameter without processes 54 µm, with processes 65 µm. 24–30 processes around circumference, 100 in hemisphere. Processes long cones with attenuated, areolated tips, 9–11 µm long, base diameter 3–5 µm, processes 3–4 µm apart, base of each process indented. Egg shell surface smooth.

Remarks. Type material could not be located (see remarks for *M. hufelandioides*) but because of the very characteristic soft spines and the description of the eggs, the identification is not in doubt. Murray's description did not include pores in the cuticle and they are difficult to discern at low magnification. They are mentioned as occurring in the

posterior region of the animal in the description of *Macrobiotus intermedius subjulietae*. However they are certainly present over the whole cuticle in the 16 paratypes examined as they are in the material from the type locality. Specimens from all sites agree well with the dimensions of that material including the five specimens from Ravensbourne and three from Lord Howe Island which had only one pair of spines above the fourth pair of legs. (Murray [1910] reported specimens with one pair of spines from Katoomba, NSW).

Habitat. The species can be found in mosses and lichens at sites from high altitudes and seems to have a preference for these substrates on rock rather than on trees.

Minibiotus scopulus n.sp.

Figs. 15, 20b; Table 14

Type material. HOLOTYPE in AM (AM KS41511): Australia, New South Wales: Galore, 35°07'S 146°47'E, 340 m a.s.l., 19 March 1994, S.K. Claxton, moss and lichen on dead trees, rock and soil in dense dry woodland. PARATYPES (7 specimens, 5 eggs in AM [AM KS41512–KS41521]; 39 specimens, 40 eggs in SKC): same data as holotype.

Additional material examined. AUSTRALIA, Western Australia: Ravenswood, 32°33'S 115°43'E, 18 February 1993, P.D. Claxton, crustose lichen on tree, 1 specimen in SKC. NEW ZEALAND: North Island, Tikitiki, 18 May 1971, D.S. Horning, 1 specimen in NZM.

Diagnosis. Smooth cuticle, yellow body cells, nine bands of pores around the body; two macroplacoids and an indistinct microplacoid; long robust claws with fine low accessory claws and thin smooth lunules.

Description. Body length 165–428 µm, pale yellow body cells, many specimens with red pigment granules in irregular bands. Eye spots present in posterior position. Cuticle smooth with round to elliptical pores (about 1 µm diameter) extending around the body in nine bands, and also on legs, becoming sparser towards the head. Buccal tube narrow (8.6% of buccal tube length). Stylet supports inserted at 66.1% of buccal tube length and ventral support long (53.2%). Pharyngeal bulb round to slightly oval, containing apophysis, two macroplacoids and a microplacoid. First macroplacoid short, solid with slight middle indentation, second macroplacoid granular with caudal bulb curved towards midline. Microplacoid indistinct and lies close to second macroplacoid. Claws robust (fourth pair of claws is 39.6% of buccal tube length) with very small refractive zone at base and short secondary branch; accessory claws short, fine and lie close to main branch. Lunules very small.

Eggs colourless to pale brown, often found in pairs, round, diameter without processes 60 µm, with processes 70 µm. Thirty-six processes around circumference and 120 in hemisphere. Processes long, thin, apparently flattened at least along the distal half. Processes mostly 6–11 µm long with a few on each egg up to 16 µm and then often bent at an acute angle; base diameter 2–3 µm and 4–6 µm between them. Shell surface dotted.

Etymology. Latin *scopulus* (masculine), observation point, projecting rock, which describes the type locality, a large monolith on the plains of western New South Wales.

Table 14. Measurements (in µm) of adults of *Minibiotus scopulus* n.sp.

Character	No.	Range	Mean	SD	SE	Holotype
body length	15	165–428	328.9	81.4	21.0	423
BT length	15	22.2–35.1	30.9	4.1	1.1	35.1
BT width	15	1.6–3.2	2.7	0.5	0.1	3.2
SI length	15	14.6–23.2	20.4	2.8	0.7	22.7
VS length	15	11.4–18.9	16.5	2.3	0.6	18.9
PR length	15	7.0–15.1	11.9	2.4	0.6	15.1
MPR length	15	6.0–13.0	10.3	2.1	0.5	13.0
m1	15	3.2–7.6	5.9	1.3	0.3	7.6
m2	15	2.2–4.3	3.4	0.7	0.2	4.3
microplacoid	15	0.5–1.6	1.2	0.4	0.1	1.6
PH length	12	25.0–42.0	34.8	5.4	1.4	38.0
PH width	12	27.0–38.0	35.1	3.9	1.1	38.0
claw I	15	7.0–11.9	10.2	1.8	0.5	11.9
claw II–III	15	7.6–12.4	10.8	1.7	0.5	12.4
claw IV	15	8.7–14.1	12.2	1.9	0.5	14.1

Remarks. The species is similar to *Minibiotus fallax* Pilato *et al.*, 1989 in having two macroplacoids, pores in the cuticle, no lunules and in the appearance of the egg. It differs from that species by not having gibbosities on the cuticle.

Habitat. The species was found in mosses and foliose lichens on rock in dense, dry woodland half way up Galore Hill but not in mosses and lichens from the top of the hill.

Minibiotus fallax Pilato, Claxton & Binda, 1989

Fig. 20c

Minibiotus fallax Pilato, Claxton & Binda, 1989: 23–26, fig. 2A–E.

Type material examined. HOLOTYPE in MM (1139-38): Australia, New South Wales, Douglas Park, 34°11'S 150°43'E, 11 January 1987, S.K. Claxton, moss and lichen on rock in open forest. PARATYPES (13 specimens, 1 egg in MM; 18 specimens, 2 eggs in SKC): same data as holotype but some also collected on 9 March 1986, 14 September 1986, 15 November 1986.

Additional material examined. NEW SOUTH WALES: Barrengarry, 34°40'S 150°30'E, 26 January 1986, S.K.C., moss on rock, cool temperate rainforest, 2 specimens. Blue Mountains, 33°43'S 150°20'E, 1000 m, 26 December 1993, 8 August 1995, 26 November 1995, S.K.C., moss on trees and rocks in closed forest, 16 specimens. New England National Park, 30°30'S 152°30'E, 1200 m, 18 December 1994, 20 April 1995, 7 January 1996, S.K.C., moss and lichen on rocks and trees in subalpine heath, 21 specimens. Jenolan, 33°49'S 150°02'E, 14 December 1986, 26 December 1992, S.K.C., moss and lichen on trees in open forest, 7 specimens. Fitzroy Falls, 34°38'S 150°30'E, 26 January 1986, S.K.C., moss and lichen in open forest, 2 specimens. Crookwell, 34°28'S 149°29'E, 29 August 1992, J. Lloyd, lichen on tree open trees, 15 specimens, 37 eggs. Taralga, 34°24'S 149°49'E, 26 April 1996, S.K.C., lichen on tree on street, 6 specimens, 1 egg. Apsley Falls, 31°03'S 151°46'E, 6 February

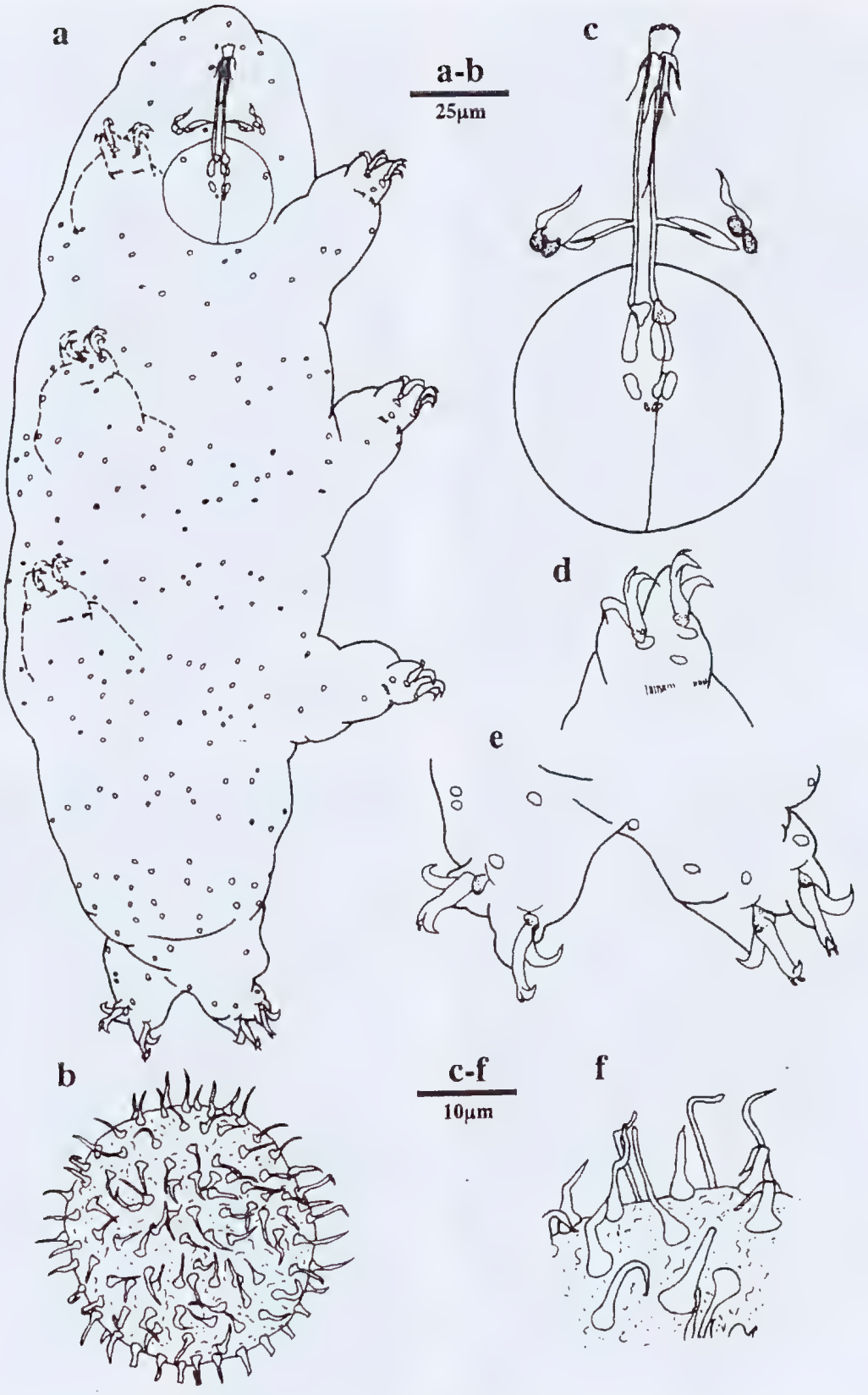

Figure 15. Taxonomic details of *Minibiotus scopulus* n.sp. **a**, habitus (paratype); **b**, egg; **c**, ventral view of the buccal armature; **d**, claws of the first pair of legs; **e**, claws of the fourth pair of legs; **f**, detail of eggshell.

1993, D. Clark, lichen on tree, 3 specimens, 1 egg. Kosciusko, 36°30'S 148°19'E, 1 October 1992, P.D. Claxton, moss and lichen on rock, 3 specimens. QUEENSLAND: Cunninghams Gap, 28°03'S 152°25'E, 3 September 1985, S.K.C., moss and lichen on trees in closed forest, 3 specimens. Ravensbourne, 27°22'S 152°08'E, 3 September 1985, S.K.C., moss and lichen on trees in open forest, 8 specimens. Crows Nest, 27°15'S 152°05'E, 3 September 1985, S.K.C., moss on rock in open forest, 3 specimens. Eumundi, 26°28'S 152°57'E, 20 December 1986 [D.S. Horning], 18 March 1994 [S.K.C.], fern on soil, moss and lichen on trees in urban park, 7 specimens. Yarraman, 26°20'S 151°58'E, 3 September 1985, S.K.C., lichen on trees in open forest, 11 specimens. Cania Gorge, 24°40'S 150°58'E, 1 April 1997, S.K.C., lichen on rock, 1 specimen. Cammoo Caves, 23°10'S 150°27'E,

Figure 16. **a**, buccal apparatus of *Minibiotus aculeatus* DIC; **b**, buccal apparatus of *Minibiotus milleri* DIC. (Scale bars = 10 μm).

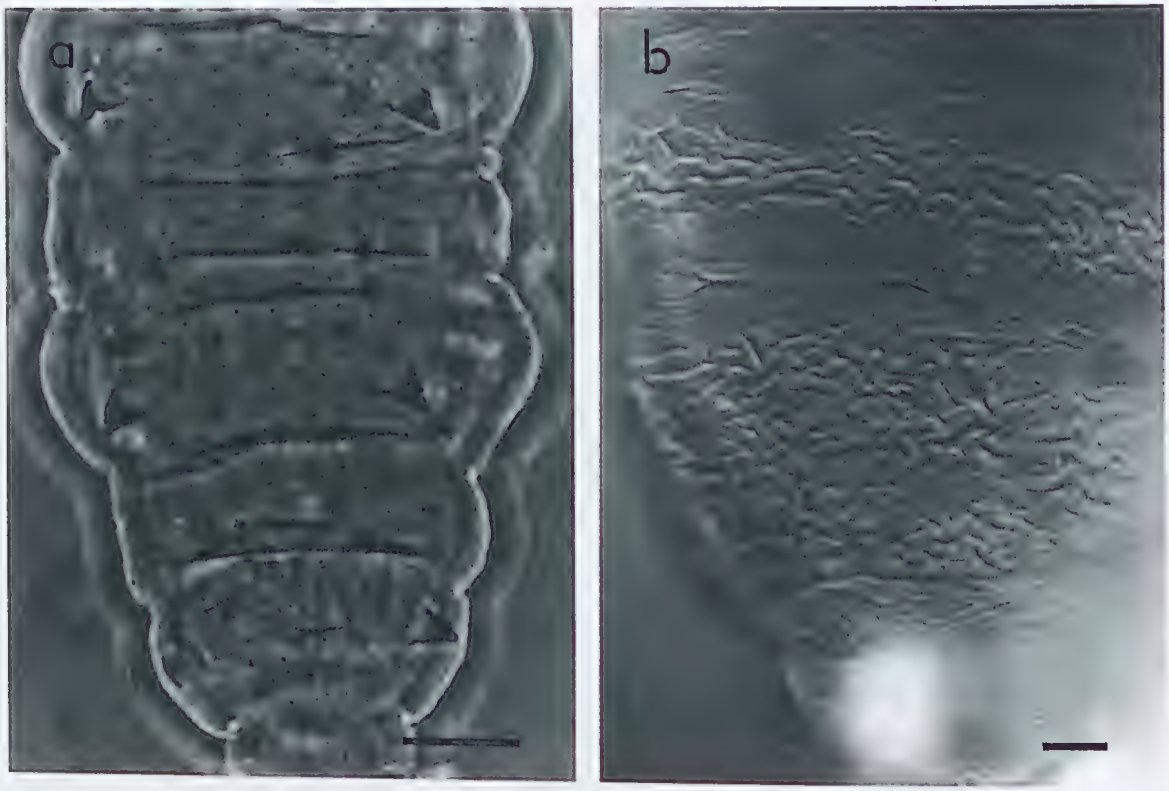

Figure 17. **a**, dorsal cuticle of *Minibiotus aculeatus* Phase; **b**, dorsal cuticle of *Minibiotus pilatus* DIC. (Scale bars = 10 μm).

1 September 1985, S.K.C., lichen on tree open field, 14 specimens. Capricorn Caves, 23°10'S 150°27'E, 2 April 1997, S.K.C., leaf litter on rock open forest, 1 specimen. All SKC.

Diagnosis. Cuticle with transverse bands of rounded gibbosities more prominent in posterior part of body, nine bands of pores around body; two macroplacoids and an indistinct microplacoid; long robust claws with high accessory claws and thin, smooth lunules.

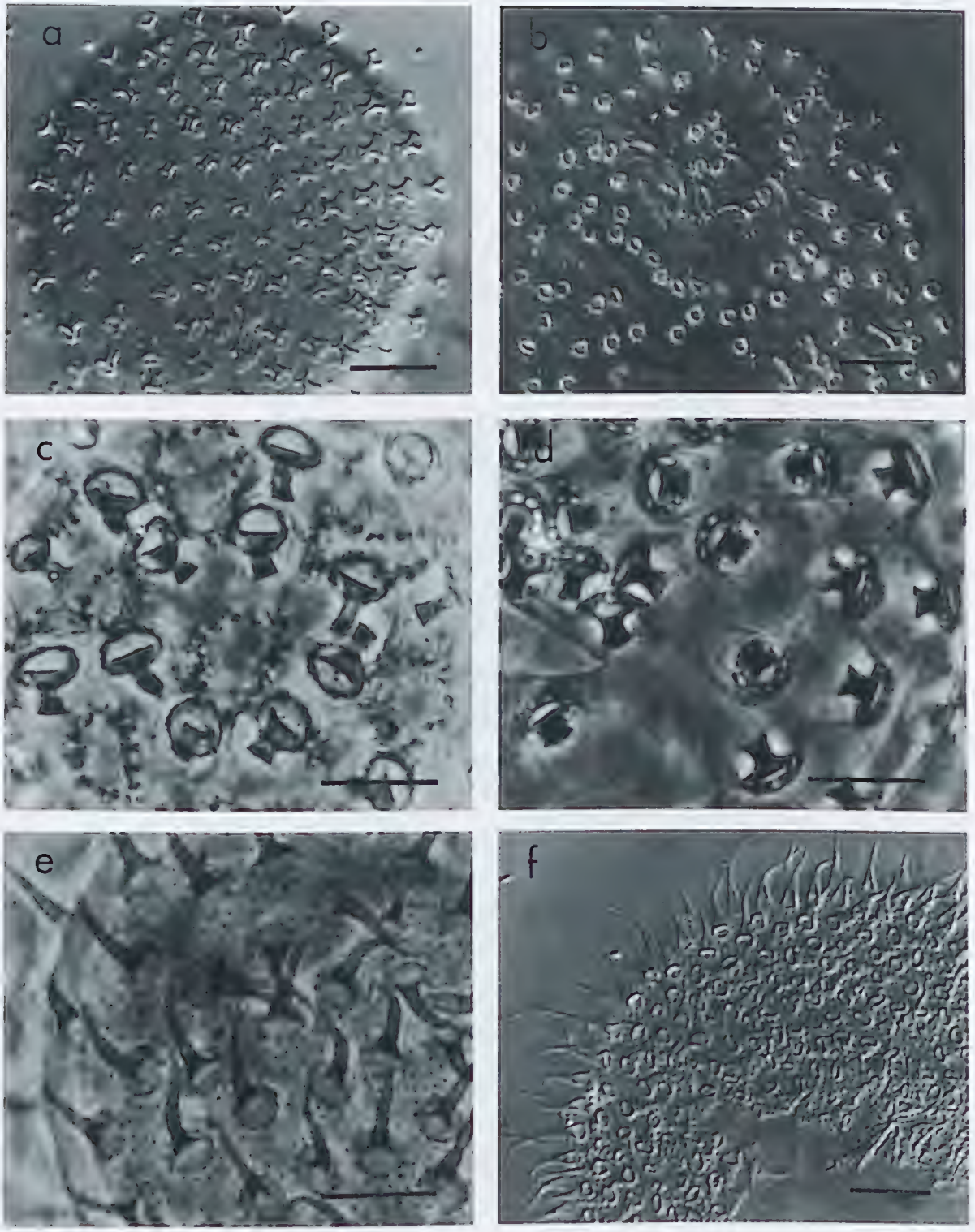

Figure 18. Eggs of **a**, *Minibiotus intermedius* DIC; **b**, *Minibiotus taiti* DIC; **c**, *Minibiotus poricinctus* Phase; **d**, *Minibiotus floriparus* Phase; **e**, *Minibiotus aquatilis* Phase; **f**, *Minibiotus hispidus* DIC. (Scale bars = 10 µm).

Emended description. Eggs colourless, found singly, in pairs and sets of four; 59–80 µm in diameter without processes, 80–100 µm with processes; 28–30 around circumference, about 100 in hemisphere; processes are strap-like with swollen bases the distal ends of which appear flattened, quite variable in height between eggs and over a single egg, most 12–16 µm but may reach 22 µm, these longer processes often swollen or bent at an acute angle near distal end, processes 3–4 µm base diameter and 2–4 µm between. Shell surface strongly dotted.

Remarks. The description of eggs is based on two egg shells found at the type locality and on eggs (including embryonate eggs) found at other localities.

Habitat. The species occurs frequently but rarely in abundance. It seems to prefer lichens on trees in dry environments.

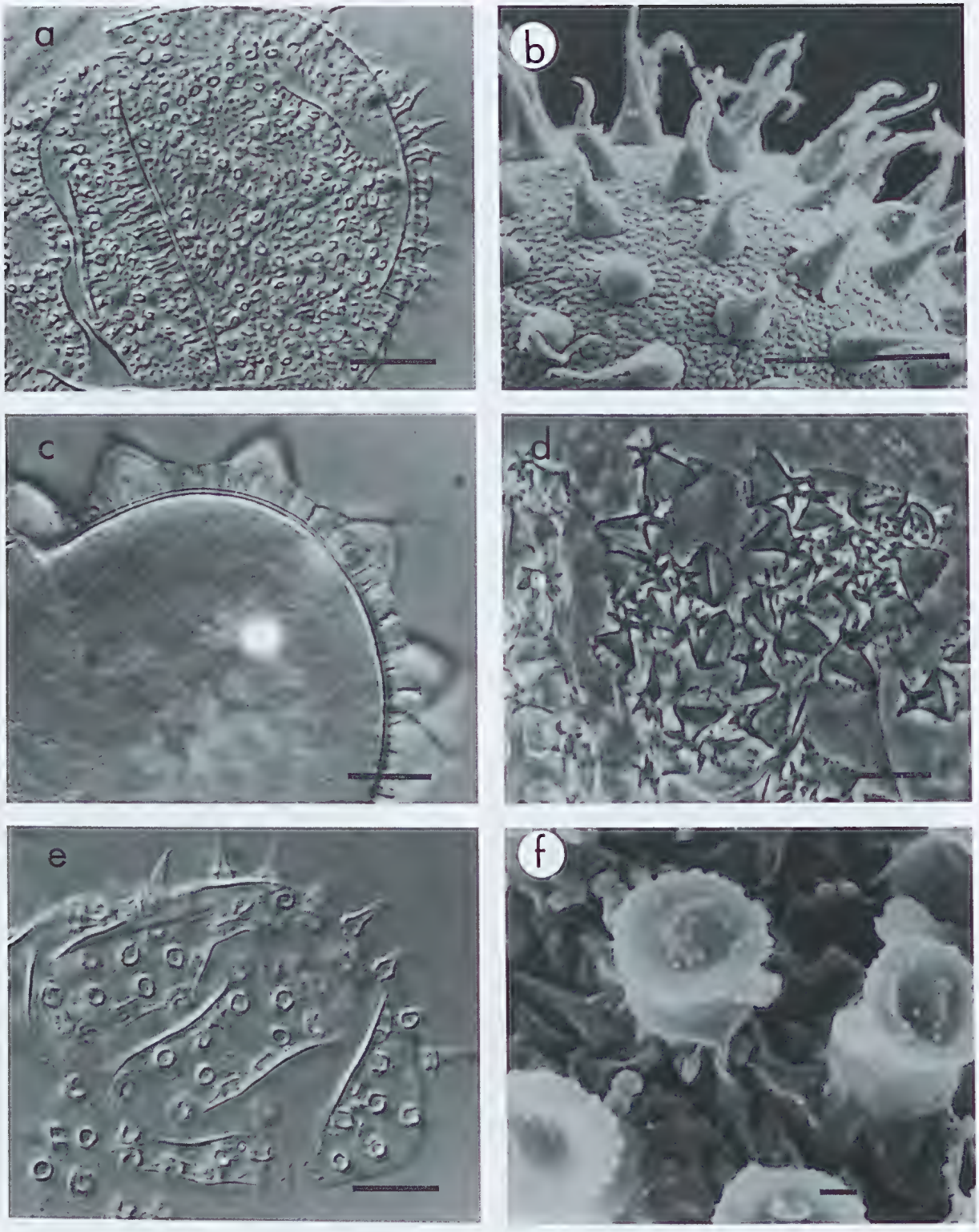

Figure 19. Eggs of **a**, *Minibiotus pilatus* DIC; **b**, *Minibiotus ethelae* SEM; **c**, *Minibiotus keppelensis* DIC; **d**, *Minibiotus asteris* Phase; **e**, *Minibiotus milleri* DIC; **f**, *Minibiotus hufelandioides* SEM. (Scale bars a–e = 10 µm, scale bar f = 1 µm).

Minibiotus maculartus Pilato & Claxton, 1988

Minibiotus maculartus Pilato & Claxton, 1988: 86–88, figs. 3A–D.

Type material examined. HOLOTYPE in MM (1019-39): Australia, New South Wales Douglas Park, 34°11'S 150°43'E, 9 March 1986, S.K. Claxton, moss and lichen on rock in open forest. PARATYPES (7 specimens, 3 eggs in MM; 61 specimens, 11 eggs in SKC) same data as holotype but some also collected on 17 May 1986, 19 July 1986, 13 September 1986, 15 November 1986 and 11 January 1987.

Additional material examined. AUSTRALIA, New South Wales: Jenolan, 33°49'S 150°02'E, 14 December 1986, S.K.C., moss and lichen on rock in open forest, 8 specimens, 8 eggs. New England National Park, 30°30'S 152°30'E, 18 December 1994, 20 April 1995, 7 April 1996, S.K.C., moss, lichen and liverwort on trees in closed forest, 26 specimens, 5 eggs. Montague Island, 36°15'S 150°14'E, 22 January 1993, D. Clark, lichen on rock exposed to salt spray, 28 animals, 3 eggs.

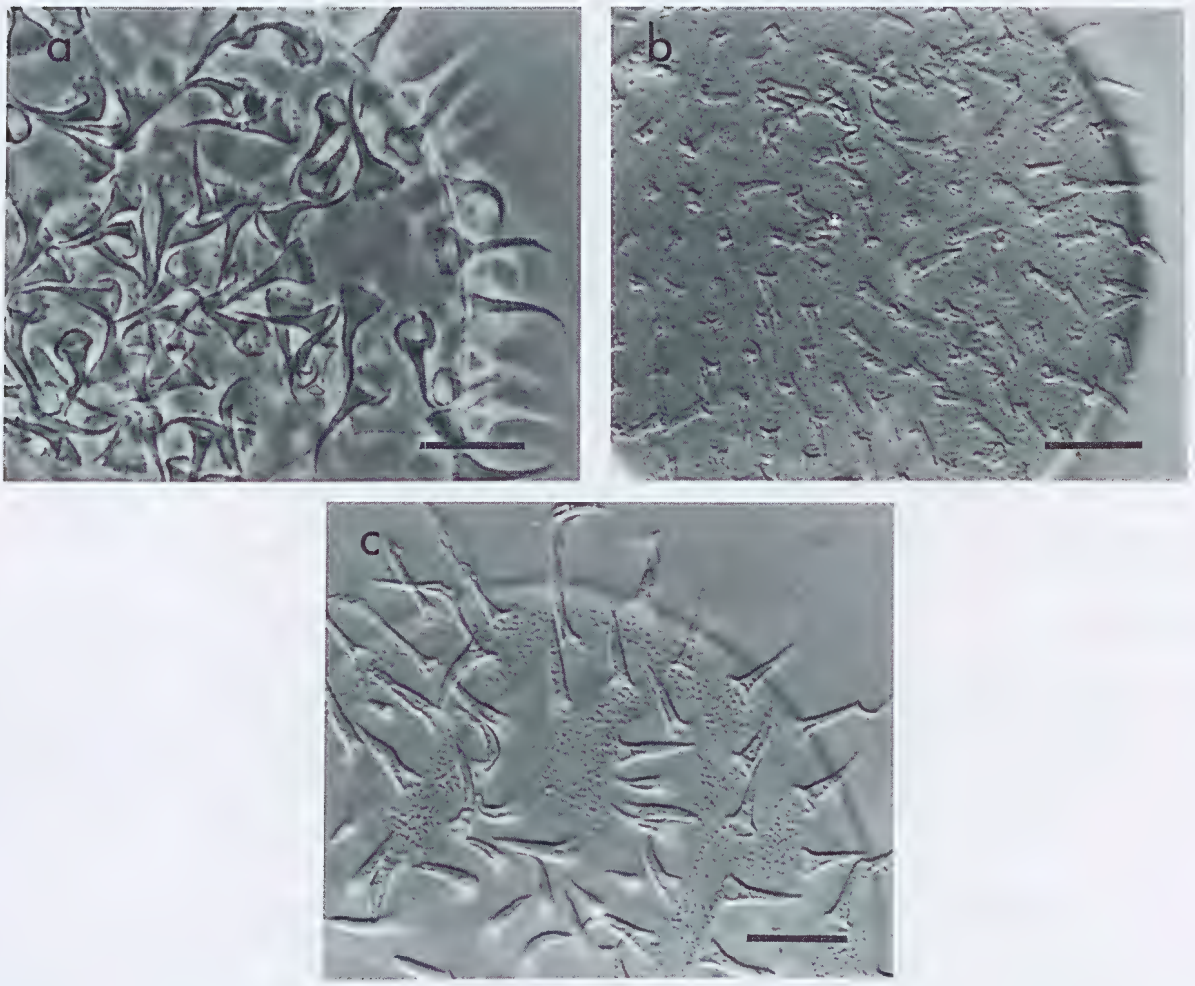

Figure 20. Eggs of **a**, *Minibiotus aculeatus* Phase; **b**, *Minibiotus scopulus* DIC; **c**, *Minibiotus fallax* DIC. (Scale bars = 10 μm).

All SKC. NEW ZEALAND: Weka Island, East Coast, 28 November 1971, G.I. Wilson, 3 specimens in NZM (NZ1136).

Diagnosis. Cuticle smooth, granulation on all legs; 3 round macroplacoids and an indistinct microplacoid; robust claws with short, high accessory claws and toothed lunules on fourth pair of claws.

Emended description. Re-examination of the type material revealed the presence of tiny teeth on the lunules of the fourth pair of claws which are 29% of the length of the buccal tube (measurement in the original description included the accessory claw).

Eggs may be quite variable in shape of the processes. In the population from Montague Island, the processes are rounded not pointed.

Minibiotus bisoctus (Horning *et al.*, 1978) **n.comb.**

Macrobiotus bisoctus Horning, Schuster & Grigarick, 1978: 236–237, figs. 114–116.

Type material examined. PARATYPE: New Zealand: Snares Islands, Penguin Rookery, 9 October 1972, D.S. Horning, 1 specimen (SA255) in NZM.

Diagnosis. Smooth cuticle with pores of irregular size and shape arranged in transverse bands, granulation on all legs; three round granular macroplacoids and an indistinct microplacoid; long robust claws with short, high accessory claws and smooth lunules.

Emended description. Body length up to 305 μm, colourless. Eyespots absent. Cuticle smooth with transverse bands of pores of irregular shape and size and granulation in small patches on outside of first three pairs of legs above claws and around claws on fourth pair of legs. Buccal tube narrow (8.3% of buccal tube length). Stylet supports inserted at 60.3% of buccal tube length; ventral support short (42% of buccal tube length). Pharyngeal bulb round containing large granular apophyses, three granular macroplacoids and one microplacoid. Macroplacoid row short (31% of buccal tube length); first macroplacoid round partly obscured by apophysis, which is about same size, second macroplacoid small, granular, and third macroplacoid granular with slight caudal bulb, which curves towards the midline. Microplacoid indistinct, lying very close to third macroplacoid. Claws long, robust (fourth pair of claws is 31% of buccal tube length). Accessory claws short, rising high above main branch. Lunules very small and smooth on all claws.

Eggs unknown.

Minibiotus furcatus (Ehrenberg, 1859)

Macrobiotus furcatus Ehrenberg, 1859: 452, fig. III. [Type locality: Monte Rosa, Italy]
Minibiotus furcatus.–Binda & Pilato, 1992: 113–115, figs. 1A,B.

Material examined. None

Emended diagnosis. Yellow body cells, smooth cuticle with variably shaped pores arranged in rows; long ventral reinforcing bar and long macroplacoid row, small indistinct microplacoid; long slender claws with short, high accessory claws and lightly toothed lunules on fourth pair of legs.

Minibiotus ramazzottii Binda & Pilato, 1992

Minibiotus ramazzottii Binda & Pilato, 1992: 115–117, fig. 1C–F. [Type locality: Rancagua, Chile].

Material examined. None

Emended diagnosis. Yellow body cells, smooth cuticle with small round pores, granulation on all legs; long ventral reinforcing bar and long macroplacoid row, distinct microplacoid; very long slender claws with short, low accessory claws and smooth lunules.

Minibiotus stuckenbergi (Dastych *et al.*, 1990)

Macrobiotus stuckenbergi Dastych, Ryan & Watkins, 1990: 61–65, figs. 6–10. [Type locality: western Dronning Maud Land, Antarctica].
Minibiotus stuckenbergi.–Dastych & Drummond, 1996: 114.

Material examined. None.

Emended diagnosis. Cuticle with small oval and large irregular pores, granulation around all claws; single dorsal transverse thickening in oral cavity; long ventral support, 3 round macroplacoids and indistinct microplacoid; slender claws with short high accessory claws and lunules with a few jagged teeth on fourth pair of claws.

Minibiotus vinciguerrae Binda & Pilato, 1992

Minibiotus vinciguerrae Binda & Pilato, 1992: 117–120, figs. 2A–E. [Type locality: Victoria Land, Antarctica].

Material examined. ANTARCTICA: Victoria Land, Pilato, 1 specimen, 1 egg in UCI.

Emended diagnosis. Smooth cuticle with variably shaped pores and fine granulation around claws on all legs; dorsal crest in oral cavity broken into teeth, long ventral reinforcing bar and long macroplacoid row, distinct microplacoid; slender claws with short, high accessory claws and smooth lunules.

Minibiotus weinerorum (Dastych, 1984)

Macrobiotus weinerorum Dastych, 1984: 400–402, fig. 14, photographs 21–25. [Type locality: Enderby Land, Antarctica].
Minibiotus weinerorum.–Miller, Heatwole, Pidgeon & Gardiner, 1994: 152–155, figs. 3A–C.

Material examined. None.

Emended diagnosis. Smooth cuticle with randomly distributed pores and granulation around claws on all legs; small round macroplacoids and indistinct microplacoid; slender claws with very high accessory claws and small, smooth lunules.

Discussion

It has become clear during this study that there are several species in the Australian fauna which may well have been identified as *Minibiotus intermedius* on the basis of older, imprecise descriptions. In order to differentiate these species a range of qualitative and quantitative characters of adult specimens were examined. Because of the small size of most of these species, observation of these characters required the highest usable power of light magnification.

Qualitative characters such as the degree of granulation around the claws, presence or absence of teeth on the lunules, the nature of the microplacoid and the length of accessory claws and their proximity to the main branch have been shown to be important in the discrimination of species and have been included in the descriptions. It should be stressed, however, that these characters might not always be visible on all specimens. Quantitative characters such as the lengths of structures of the buccal apparatus and of the claws have been given for the different populations of species and such measurements are considered to be essential for the description of any species in this genus. Ratios (*pt*) have been generated from these measurements (Table 15) and some of these are particularly effective in discriminating species, e.g. stylet support insertion point, ventral support length and claw length. Similar ratios have been used to discriminate species of the *hufelandi* group of the genus *Macrobiotus* (Bertolani & Rebecchi, 1993).

A group of species found in this study with very similar morphology (smooth cuticle and granulation around the claws) can be readily differentiated on the basis of the appearance of their distinctive eggs. However, when the egg cannot be found, as is often the case in the study of tardigrades, the use of a full range of adult characters becomes very important. Likewise, there is a group of species whose egg morphology is very similar (long thin processes) and it is important to report fully a range of qualitative and quantitative characters of the eggshell and the processes.

Table 15. Number of observations (n), mean and standard deviation (SD) of *pt* values for some characters of *Minibiotus* species with three macroplacoids. SIL—stylet support insertion level; VS—ventral support length; BTW—external buccal tube width; MPRL—macroplacoid row length; and CLIV—claw length on fourth pair of legs excluding or including (*) accessory claw.

species	n	SIL mean	SD	VS mean	SD	BTW mean	SD	MPRL mean	SD	CLIV mean	SD
M. intermedius	20	55.0	0.9	37.3	2.0	6.8	0.5	26.5	1.5	24.8	1.8
M. taiti	20	60.3	0.3	40.3	0.7	8.0	0.3	32.1	1.6	33.2	0.8
M. poricinctus	20	59.5	0.4	35.8	0.9	7.6	0.4	30.9	1.4	27.3	0.7
M. floriparus	19	64.4	0.7	46.1	3.8	7.6	0.7	33.1	1.9	34.0	1.6
M. aquatilis	16	68.3	0.2	53.0	0.8	9.0	0.4	37.9	1.9	34.6	2.2
M. hispidus	10	65.2	0.5	45.7	1.5	8.0	0.2	33.2	1.1	28.1	0.8
M. pilatus	7	67.9	0.5	48.1	0.4	7.9	0.4	30.4	2.7	29.7	0.8
M. ethelae	8	64.9	1.2	51.4	1.2	7.6	0.2	32.3	0.8	37.6	0.7
M. keppelensis	12	60.6	0.9	40.4	1.6	5.8	0.2	26.6	1.0	30.1	1.2
M. asteris	20	63.8	0.7	44.8	0.9	8.0	0.5	30.0	1.8	28.1	0.9
M. milleri	20	73.0	0.7	36.4	1.0	9.7	0.3	37.0	1.1	26.5	0.8
M. hufelandioides	16	67.4	0.5	45.9	2.0	8.6	0.4	38.2	1.1	29.3	1.2
M. aculeatus	7	63.7	1.1	51.4	1.5	7.8	0.3	32.2	2.0	22.8	0.9
M. maculartus	14	64.4	0.6	53.0	1.3	8.1	0.6	31.5	1.8	29.2	1.3
M. bisoctus	1	60.3		42.0		8.3		31.0		31.0	
M. furcatus		68.4		62.0		7.9		36.5		38.6*	
M. ramazzottii		68.2		61.5		11.6		42.4		48.1*	
M. vinciguerrae		67.4		59.0		9.9		37.3		41.6*	

The description of *M. taiti* and *M. poricinctus* presented here and examination of specimens from a number of countries, suggests that there are many species in the *intermedius* group, that is, species in which the adult form is very similar and whose eggs bear processes which could be described as screw-shaped and are surrounded by a membrane. This work suggests that many reports of *M. intermedius* in the literature may be inaccurate. Bertolani & Rebecchi (1993) have described a parallel situation for the *Macrobiotus hufelandi* group.

A major difficulty in tardigrade taxonomy has been the lack of sufficient detail in older descriptions of species and the lack of type material for them. Consequently it is almost impossible to decide on the correct identification for some species. As an example, the description of *Macrobiotus crassidens* Murray, 1907 suggests that it is very similar to *Minibiotus hispidus* although there appear to be sufficient differences to warrant the description of the latter as a new species. Other species of *Macrobiotus* almost certainly belong to the genus *Minibiotus* e.g., *Macrobiotus acontistus* De Barros, 1942 and *Macrobiotus marcusi* De Barros, 1942. Seventy four slide mounted specimens from Venezuela labelled *Minibiotus intermedius* and deposited in the Bohart Museum were examined. Forty nine of those specimens conform to the description of *M. intermedius* supplied in this paper. Five specimens appear to belong to the taxon *M. marcusi* and 11 specimens to *M. acontistus*. These have not been described in this paper because they are not from the type locality (both Sao Paolo, Brazil) of either species and there were no eggs accompanying them.

Of forty four slide mounted specimens from New Zealand labelled *M. intermedius* and deposited in the Museum of New Zealand only two actually conform to the above description. The other specimens belong to seven other taxa including six Australian species and an unknown species. The last was not described here as there were no eggs included.

Binda & Pilato (1992) observed that all species of *Minibiotus* have double curvature of the buccal tube. However in this study, three species, *M. hufelandioides*, *M. aquatilis* and *M. milleri*, were found not to have a curve in the buccal tube as it enters the pharyngeal bulb. Other characters considered by these authors to be generically significant are—stylet supports inserted a considerable distance from the pharyngeal bulb, short reinforcing bar and the first macroplacoid always situated very close to the apophysis. With the examination of many more species in the present work it is possible to be more precise and to set out *pt* values which discriminate this genus from the closely related *Macrobiotus* as shown in Table 16. In addition, the following characters—antero-ventral mouth, teeth in the oral cavity absent or reduced, extra thickening of the buccal tube wall immediately below the point of insertion of the stylet supports have been found to be consistent among species of *Minibiotus*.

Table 16. Length or width ratios relative to length of the buccal tube expressed as a percentage (*pt*) for species in the genera *Minibiotus* and *Macrobiotus* with three macroplacoids.

	Minibiotus (18 species)	*Macrobiotus* (19 species)
stylet insertion length	≤ 73	≥ 74
ventral support length	≤ 62	≥ 65
buccal tube width	≤ 12	≥ 13
macroplacoid row length	≤ 42	≥ 42

ACKNOWLEDGMENTS. I would like to thank Dr M.G. Binda and Dr G. Pilato for their observations on *Minibiotus ethelae* n.sp. I would also like to thank Mr R. Palma for loan of New Zealand material, Dr H. Dastych and Dr B. Lawrence for loan of South African material and Dr L. Baptiste (Bohart Museum) for the loan of South American material. Thanks also to Mr N. Marley, Dr W.R. Miller, Dr R. Bertolani, Mr B. Grabowski, Dr V.I. Biserov, Dr C.W. Beasley and Dr M.C. Claps for the loan of material from other countries. I thank Antonius Moscal for access to a large collection of Tasmanian mosses. I also thank Peter Claxton for his encouragement and critical comments on the manuscript. This work was supported by a Macquarie University Postgraduate Research Scholarship and by a travel grant from the Centre for Biodiversity and Bioresources, Macquarie University. This is paper number 240 of the Centre for Biodiversity and Bioresources, Macquarie University. This paper was presented at the Sixth International Symposium on Tardigrada, Selwin College, Cambridge, UK, 22–26 August 1994.

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The Distribution and Biology of *Patiriella vivipara* (Echinodermata: Asteroidea: Asterinidae) a Sea Star Endemic to Southeast Tasmania

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ABSTRACT. The asterinid sea star *Patiriella vivipara* is endemic to southeast Tasmania and has a highly restricted distribution, being only known from four locations. It has an unusual pattern of viviparous reproduction, giving birth to juveniles. In this study the birth rate, growth rate, size and age at commencement of reproduction of *P. vivipara* was examined in aquaria for a period of six years. The population of *P. vivipara* at Pittwater was also monitored through monthly examination of a permanent $1m^2$ quadrat in which the number of adults and juveniles were counted and recorded. These counts were made over an eight-year period. *Patiriella vivipara* gives birth to juveniles through the year with a period of enhanced reproduction from November to January. Records of water salinity and temperature were taken at Pittwater, as were air temperatures and exposure times during low tide.

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Patiriella vivipara (Dartnall 1969) (Asterinidae) is a small 5 armed asterinid sea star that incubates its young in the gonads (Dartnall 1969; Byrne 1991, 1996). When first described (Dartnall, 1969) it was the only known species of sea star to exhibit viviparity. Three other viviparous asteroids were subsequently found and these are also asterinids. They are *Asterina pseudoexigua pacifica*, (Hayashi, 1977) from Japan, *Patiriella parvivipara*, (Keough & Dartnall, 1978) from South Australia and *P. pseudoexigua* from Queensland, (Byrne, pers. comm.). *Patiriella vivipara* is a simultaneous hermaphrodite and most of the gonads are ovotestes, thereby creating the potential for self fertilisation (Byrne, 1996). The juveniles emerge through the gonopores which are located on the aboral surface. It is not known whether self, cross fertilisation or both takes place. An unusual feature of *P. vivipara* and *P. parvivipara* is that intragonadal cannibalism supports post-metamorphic growth to an advanced size (Byrne, 1996).

Patiriella vivipara is endemic to southeast Tasmania, and has a highly restricted distribution. In the original survey (Dartnall, 1968) this species was recorded from only three localities, Pittwater, Roches Beach and Eagle Hawk Neck. In 1990 another colony was found on the southern shore of Fortescue Bay (Fig. 1). *Patiriella vivipara* is a uniform orange/yellow orally and aborally, has a maximum radius (R) of 15 mm and the average adult size is approximately 10.00 mm R.

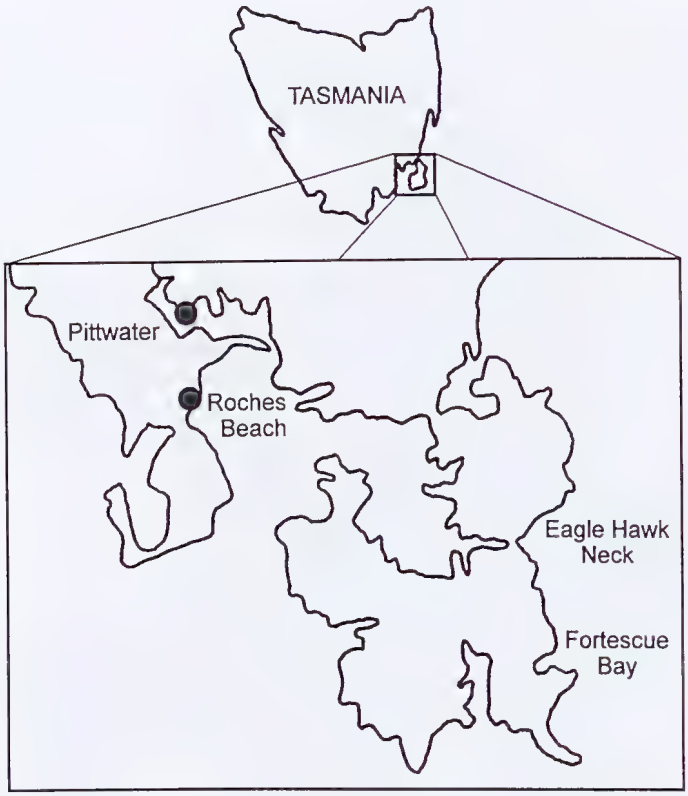

Figure 1. Locality map for *Patiriella vivipara* in south-east Tasmania.

Viviparity in *P. vivipara* represents the most derived life history pattern in the Asteroidea, and provides important insights into the evolution of development (Byrne, 1996; Byrne & Cerra, 1996). *Patiriella* is a specious genus in Australia (Dartnall, 1970) and their divergence was associated with developmental change (Byrne, 1995; Byrne & Cerra, 1996; Hart, *et al.*, 1997). Considering the highly restricted distribution of *P. vivipara*, its non-dispersive life history and its scientific importance, this study provides essential information for the conservation biology of this unique sea star.

Methods

In this study reproduction and growth of *Patiriella vivipara* was documented in aquarium and field observations spanning a eight-year period from 1975 to 1983. The population of *P. vivipara* on the shore was also monitored at Pittwater (42°48'S 147°32'E), Eagle Hawk Neck (43°01'S 147°55'E) and Roches Beach (42°54'S 147°30'E). The length of shoreline at all sites occupied by this asteroid was estimated by noting the presence of the asteroids while measuring the distance walked along the shore. During 1995 the population on the southern shore of Fortescue Bay (42°08'S 147°57'E) was examined, and the length of shoreline occupied by *P. vivipara* was also measured. Emphasis was placed on the Pittwater site because this has the largest known population of *P. vivipara*.

The population of *Patiriella vivipara* at Pittwater was examined on the shore and in aquaria. From 1976 to 1982 specimens were maintained in glass aquaria to determine growth rate, size at first reproduction, birth rate and potential for reproduction in isolation. The sea stars fed on an algal film that formed on the walls of the aquaria. For the growth rate study, five juvenile *P. vivipara* (radii 1.25–2.25 mm), were followed for up to six years. They were placed in aquaria in isolation and periodically removed to measure their radius (R) from the centre of the disc to the end of the arm. These sea stars were also used to determine the potential for reproduction in isolation, and the aquaria were monitored for the appearance of new juveniles. The size at which these *P. vivipara* produced their first young was recorded. For the reproductive output study, six adults (R = 9.0 mm) were placed in each of two aquaria and the number of juvenile births recorded.

The population of *Patiriella vivipara* at Pittwater was censused at approximately monthly intervals from 1976–1983. Each month the number of individuals in a fixed 1 m^2 quadrat was counted and their radii measured. The quadrat was sited at the base of the rockfill along the southern side of the eastern causeway and was marked by rocks on a gently sloping area of the rockfill.

Several environmental parameters were measured at the area in Pittwater occupied by *P. vivipara*. These included air and sea temperature and water salinity. Water salinity and temperature were recorded on a monthly basis approximately 1.5 hrs before or after high tide, using a salinity/temperature meter. *Patiriella vivipara* can be emersed for several hours at low tide and so the air temperature was recorded from a thermometer set up at my home. The length of time that the sea stars were emersed during the low tide was recorded by noting the time with a watch.

Day and night feeding activity of *P. vivipara* at Midway Point in the Pittwater area was also examined. This involved documentation of the position of the sea stars on top of or under rocks, and whether they had their stomachs extruded.

Results

Distribution and habitats

The sites where *Patiriella vivipara* occurred are shown in Fig. 1. At each site *P. vivipara* was found only in the upper area of the intertidal zone. At Pittwater this sea star was found among or under loose rock on a gently sloping sandstone shelf (Figs. 2a–c), and at a maximum depth of 1.5 m at H.W.S. The shore in Upper Pittwater where the main concentration of *P. vivipara* occurred (Fig. 1) consisted of approximately 50% sand or sandy mud and 50% sandstone shelf. Lower Pittwater was mostly sand or sandy mud, except for a small area of sandstone on the southern end of Midway Point where *P. vivipara* could be found (Figs. 2a–c). Two causeways, approximately 1 km long, link Midway Point to the western and eastern shores of Pittwater respectively. Just below high water, *P. vivipara*

occurred in a narrow band on the sandstone and basalt rocks used to construct the causeways. Pittwater is a sheltered bay opening to the open sea by a narrow channel at the south-east corner. Pittwater had the largest population of *P. vivipara*, comprised of several thousand specimens. At this site *P. vivipara* inhabited approximately 5 km of the shoreline.

At Roches Beach (Fig. 1) the population of *P. vivipara* was limited to a sandstone shelf approximately 100 m^2 that protrudes out from the middle of a sandy beach. Although Roches Beach is a relatively sheltered site, the rock shelf can be subjected to considerable wave action at times, dependent upon the wind direction. There was a good cover of loose rocks where *P. vivipara* could shelter. Here *P. vivipara* only inhabited the inshore northern quarter of the rock shelf in an area roughly 35 m^2. In 1983 the population was estimated to be comprised of approximately 400 animals.

The Eagle Hawk Neck (Fig. 1) site differs from the other two locations in being a large platform of sedimentary rock on the open (eastern) coast where it is exposed to Tasman Sea conditions. A well known tourist attraction (*The Tessellated Pavement*), the site has an estimated population of 1500 *P. vivipara* sheltered amongst carpets of the small mussel *Xenostrobus pulex*. During calm sea conditions in the summer months specimens were occasionally found in the open in pools on the pavement. At Eagle Hawk Neck a second population of *P. vivipara* is located about half a kilometre to the north of *The Tessellated Pavement*. Here *P. vivipara* were found on the rock platform under rocks. Their numbers were difficult to estimate due to the size and placement of the rocks. The combined length of shoreline inhabited by *P. vivipara* at Eagle Hawk Neck was approximately 300 m.

In 1995 a survey of the population of *P. vivipara* at Fortescue Bay (Fig. 1) was undertaken. At this location *P. vivipara* inhabited the southern shore well in from the entrance to the bay. On this rocky shore *P. vivipara* occupied a narrow band just below high water mark and was found well down into the rocks. This last survey estimated the number of animals at this site to be approximately 50. The approximate length of shoreline inhabited at Fortescue Bay by *P. vivipara* was 200 m.

Figure 2. a, A sandstone substrate with loose littered rocks; type locality for *Patiriella vivipara* at Midway Point, Pittwater, Tasmania, 42°49'S 147°31'E. **b**, Type locality, Pittwater, low tide. **c**, Adult and juvenile *P. vivipara* at Pittwater on the under surface of a rock (×0.6).

Environmental conditions at Pittwater

Sea water salinity and temperature and air temperature were measured monthly at Pittwater from 1979 to 1983. At this site, *P. vivipara* contended with a wide range of climatic conditions. When exposed during spring tide, they were out of water for as long as 7 hrs. During this time air temperature extremes ranged from -3°C in winter to 40°C in summer. *Patiriella vivipara* also tolerated rainfall during low tide. Sea water temperature also varied considerably throughout the year, with the minimum 3.5°C recorded in July 1982 and the maximum 34°C recorded in February 1977 and February 1982.

The salinity at Pittwater averaged 32‰, but varied depending upon rainfall. The main sources of fresh water were from five small creeks or rivers, run off from surrounding hills, and drainage from the townships of Sorell, Midway Point and Lewisham.

Figure 3. Population count for *Patiriella vivipara* at Pittwater, 1976 to 1983.

Pittwater population

Although sandy mud dominated the shore at Pittwater, *P. vivipara* was rarely seen on this substratum. The sea stars could not attach their tube feet to this material, nor could they right themselves if placed with their aboral surface on the sandy mud. Adult *P. vivipara* adhered strongly to the top or underside of rocks located on the sandy mud. Juvenile *P. vivipara* were rarely seen on the top of rocks, and when present were readily dislodged by disturbance.

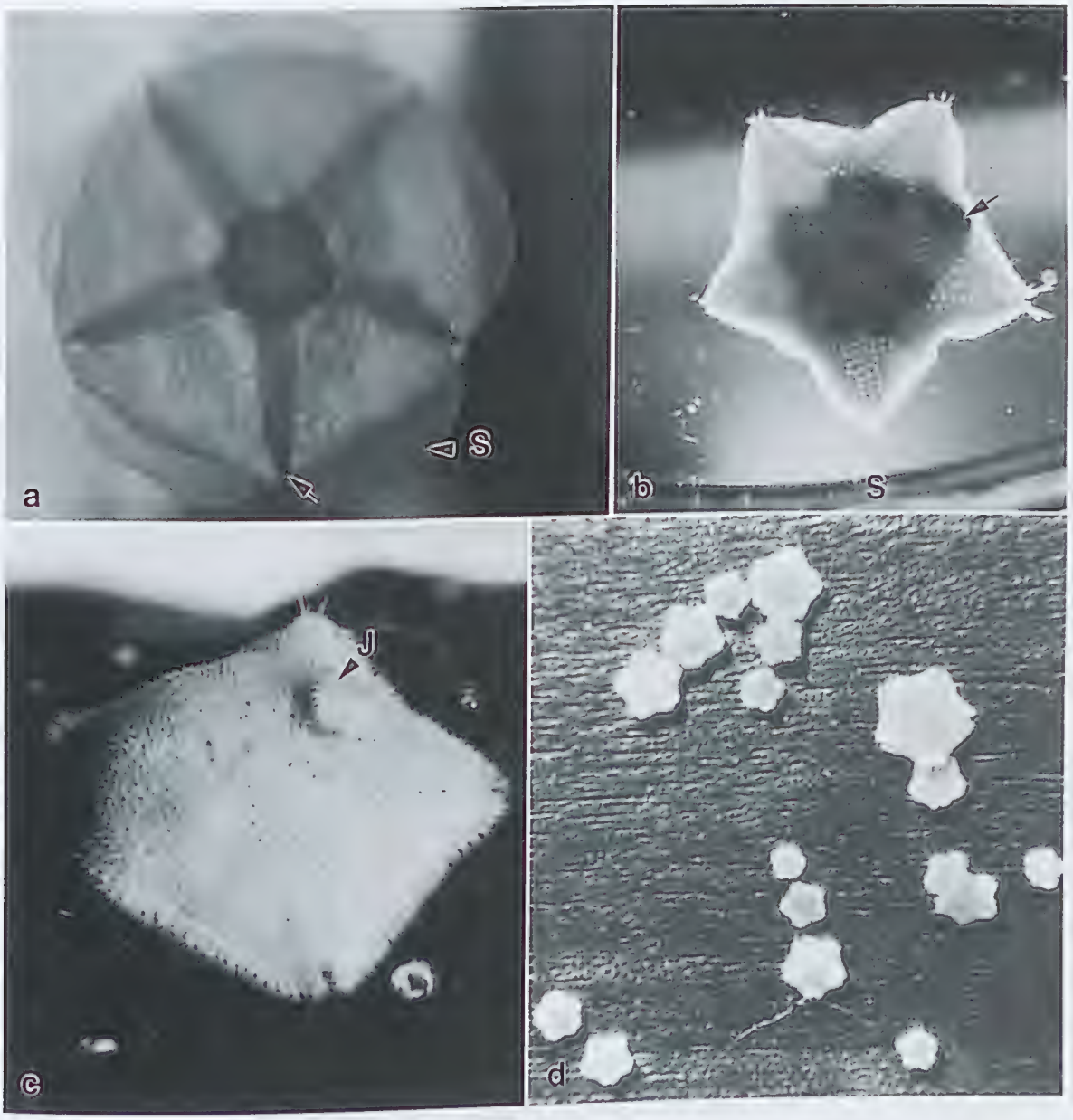

Figure 4. **a**, Adult *Patiriella vivipara* feeding on an algal film on the aquarium wall, showing the stomach (s) everted beyond its body, retaining a grip with the outermost pairs of tube feet (arrow) (×3.5). **b**, A back lit adult. The central dark area is the stomach. Arrow points to a well-developed gonad (×2.5). **c**, Adult in the process of giving birth. The juvenile (J) is about halfway out of the gonopore (×3). **d**, A selection of juveniles, born in aquaria, ranging in arm radius from 1.00–4.00 mm (×2).

Figure 3 shows the number of adults and juveniles counted in the selected 1 m^2 area on the eastern causeway from May 1976 to December 1983. In this figure sea stars R<5.0 mm are classed as juveniles because 5 mm is the minimum size of parents observed to give birth.

Feeding activity

Patiriella vivipara fed on the algal film and associated micro-organisms that grew in the aquaria and on the rocks on the shore (Fig. 4a).

On the shore, feeding activity was influenced by weather and tidal conditions, with most activity taking place between dusk and dawn. Feeding also occurred during the day providing the weather was dull, at which time *P. vivipara* came on to the top of the rocks to feed. Juveniles (R<5.0 mm) were rarely seen feeding on top of rocks.

In aquaria, feeding seemed to be a continuous process, especially during the summer. In colder months feeding activity was reduced, and on very cold days, virtually ceased.

Growth rate

The growth of six juveniles was followed from 1976 to 1981. In 1976 the radius of the juveniles were measured

when put into the aquarium on 1 January and again at the end of December. At the beginning of these growth trials the juveniles had a mean radius of 1.96 mm (SE = 0.03, range 1.0–2.5 mm, n = 6). Subsequent measurements were taken on 31 December of each year, depending on their survival. The growth recorded for the juveniles ranged between 2.75–6.50 mm for year 1 (X = 5.3, SE = 0.56, n = 6); 0.25–3.25 mm for year 2 (X = 1.6, SE = 0.45, n = 6); 0.00–0.75 mm for year 3 (X = 0.5, SE = 0.18, n = 4). In years 4–5 there was only one surviving specimen and it grew 0.25 mm in year 4, 1.00 mm in year 5 and 0.00 mm in year 6. During the first 12 months *P. vivipara* juveniles exhibited a faster rate of growth compared to later years.

The growth of an additional four juveniles was monitored from November 1978 to December 1980. At the start they had a radius of 1.50 mm (n = 4), and at the end of two years they had a mean radius of 6.125 mm (SE = 0.36, n = 4).

The life span of *P. vivipara* is not known. Four specimens lived six years in the aquaria before dying as the result of a heat wave. When collected they were estimated to be two years old, making them eight years old when they died. Just prior to the heating event, they were still healthy and reproducing.

Reproduction

During the years 1976 to 1983, a total of 4429 adult and 7517 juvenile *P. vivipara* were counted in the 1 m^2 quadrat located on the eastern causeway, a ratio of 1.7 juveniles per adult (Fig. 3). Juvenile births could not be followed in detail and so the actual number of births is not known. *Patiriella vivipara* reproduced throughout the year, with the greatest number of juveniles appearing in spring and summer (October to January), in most summers monitored (Fig. 3). The high number of juveniles obtained in June and July of some years suggest that there may also be a mid-year release period.

Six sea stars, having an average radius of 9 mm, were placed in each of two aquaria and records of juvenile births were kept until all adults had died. One aquarium operated from January 1976 to July 1979, producing a total of 119 juveniles, an average of five juveniles per adult per year. The second aquarium operated from February 1976 to March 1981 producing 333 juveniles, an average of nine juveniles per adult per year. Adults maintained in aquaria for up to eight years continued to produce juveniles.

Patiriella vivipara has 10 sets of gonads situated interradially in pairs. It is possible to hold a sexually mature specimen up to a bright light and—through the oral surface—see and count sets of gonads containing developing juveniles (Fig. 4b). These will be visible as a dark orange dot. As the juvenile develops, a small dark orange bump appears on the aboral surface of the parent over the developing set of gonads (Figs. 2c, 4b). When birth is imminent, the centre of the bump changes from dark orange to white. Initially it was thought that the skin above the juvenile split at birth, but it is now known that the juveniles emerge through the gonopores (Byrne, 1996).

During birth which can take as little as 2 hrs or as long as 48 hrs, the juvenile emerges without any apparent assistance from the parent (Fig. 4c), which moves around the aquarium normally. Stillborn juveniles have been recorded so the parent must have some means to expel moribund progeny. Once the juvenile is free, it either walks or rolls down the aboral surface of the parent. If the parent is on the side of the aquarium or upside down under a rock, the juvenile drops gently to the bottom. If the juvenile lands upside down, it rights itself, immediately taking up an independent life. At birth the juveniles ranged in size from 0.30 mm to 5.0 mm R with 1–8 pairs of tube feet (Fig. 4d). The majority of newly emergent juveniles were approximately 1.50 mm R with 4–5 pairs of tube feet.

Patiriella vivipara is capable of reproduction in isolation, the time before the first births took place ranged from 14–42 months and the average was 22 months. Whether self fertilisation or parthenogenesis took place is not known. The minimum size of the parent giving birth was 5.00 mm R. Some sea stars did not produce juveniles until they had attained a radius of 7.00 mm. Four juveniles born in November/December 1978 were placed in an aquarium on 1 January 1979 to determine if juveniles from an isolated parent would reproduce. The first juveniles were born in February 1981, approximately 27 months after the birth of their parents.

Occasionally adults were observed to suddenly give birth to a number of juveniles in a very short period. This happened during a time of stress when the water temperature increased to 30°C and above during a sudden onset of hot weather, and was possibly associated with decreased oxygen levels. High or low salinity extremes, can also cause "stress births". The highest number of juveniles born to a single adult was 15 in 24 hrs, and from an aquarium containing six adults, was 23 in 24 hrs. All these juveniles were sufficiently developed to survive, and ranged in radius from 0.75–2.00 mm. Although the maximum number of juveniles born in a short time from a single aquarium-held adult was 15, dissection of several adults indicated that this number could be higher. The specimen, (R = 9.5 mm), illustrated in (Fig. 5) contained 66 juveniles, the majority of which could survive if born at this stage in sheltered conditions on the shore.

A diseased sea star (see below) will also "stress birth" especially if the disease is terminal. The juveniles born under these circumstances are mostly premature, and do not survive long. However, the first 3–4 born are generally large enough to survive.

Morphological variation

Morphological variation in *Patiriella vivipara* is common, with 3-, 4- or 6-arm sea stars present on the shore (Fig. 6a). Juveniles having these arm numbers were also born in aquaria. At reproduction these individuals in turn give rise to progeny with a similar number of arms, or the normal complement of five arms. The percentage of morphological variations to the number of births is low. Out of 452 juveniles born in the aquaria, one had two arms, 12 had three arms, 18

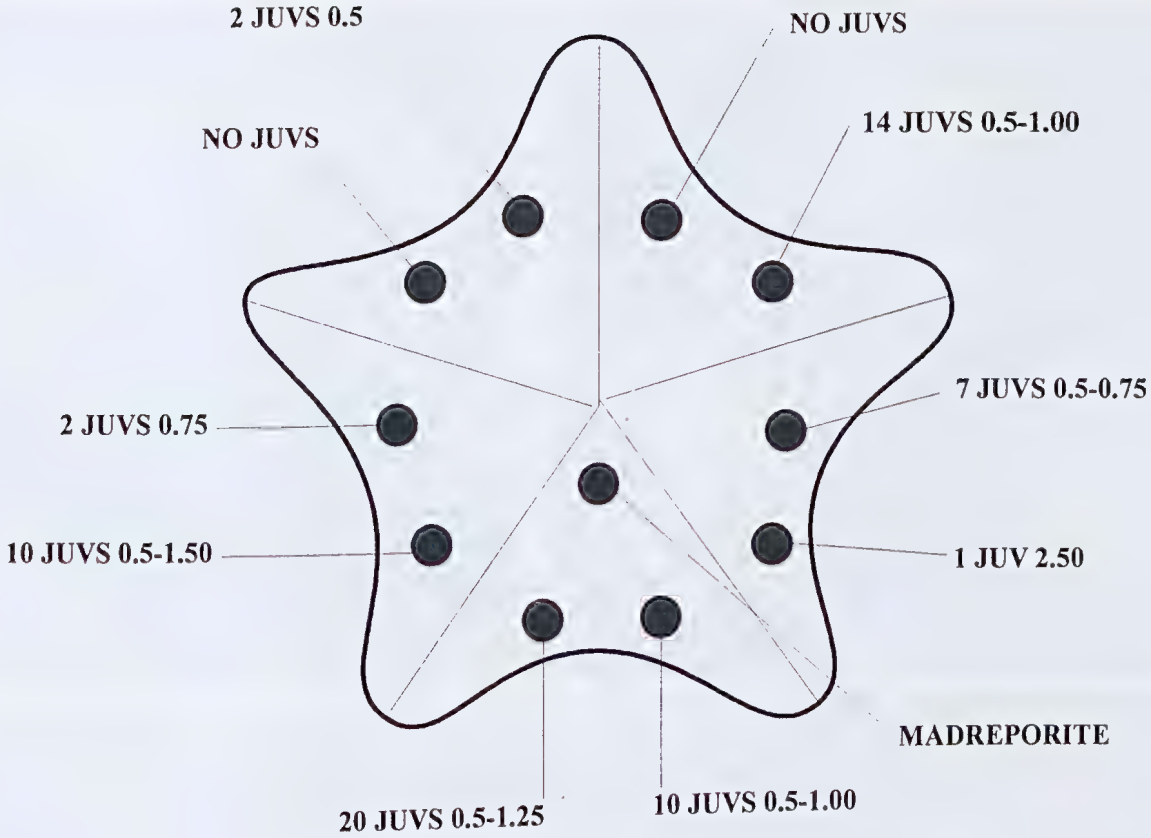

Figure 5. Diagrammatic view of a dissection of an adult *Patiriella vivipara* showing the number of recognisable juveniles in each gonad.

had four arms and four had six arms. These non-pentamerous juveniles were 7.08% of the total births. On the shore the percentage is lower, about 2.5% (n = 188).

A two-armed juvenile born in an aquarium survived for five months (Fig. 6b). At birth it was 2.25×11.50 mm along the major axes, and could move around in a fashion. For the most part it rocked in place, and when it did advance it followed a zigzag path. Although it was able to feed on the algal film, it had difficulty in everting its stomach. When it died, it measured 3.50×2.50 mm along the respective axes.

Disease

Patiriella vivipara is commonly affected by "brown spot" disease (Figs. 6c–d). Brown spot disease may or may not be fatal to the sea star, depending upon its severity. In specimens with this disease, small brown areas are evident on the aboral surface and occasionally on the oral surface. This disease (Figs. 6a,c) was seen on numerous specimens on the shore and in aquaria and at all times of the year over the eight years of study. It can be one small spot that clears in a few days, or it can remain for two to three months. In mild cases this disease clears without leaving a scar. During a moderate attack, several spots of varying sizes can appear. Some of these, especially the larger ones can cause a small amount of necrosis of the tissue, which heals, leaving a scar (Fig. 6d). In severe cases, necrosis progressed until the sea star dies. This is a slow death, taking up to four weeks.

Discussion

Patiriella vivipara along with *P. exigua, P. pseudoexigua* and *P. parvivipara* belong to the "*exigua*" group proposed by Dartnall (1970). The diagnostic characters of the group include the presence of five rays, single oral intermediate spines, and aboral spines on the centre of the disc being 0.2–0.3 mm long. The arm length of these species is seldom greater than 15.00 mm R (Dartnall, 1970). *Patiriella vivipara* is an extra-oral feeder on micro-algal surface films and can evert its stomach to a diameter larger than that of its body while feeding. This method of feeding has also been reported for *P. exigua* (Branch & Branch, 1980; Arrantes & Underwood, 1991), *P. parvivipara* (Byrne, pers. comm.) and the closely related species *Asterina gibbosa* (Crump & Emson, 1978). Like *P. vivipara*, *A. gibbosa* comes out from under the rocks at night to feed on the upper surfaces (Crump & Emson, 1978). *Patiriella exigua* differs from *P. vivipara* in that its distribution is not restricted to rock shelter. This species was abundant on intertidal rock platforms where its feeding activity was observed to occur through the day. Neither *P. vivipara* nor *P. exigua* completely remove the algal growth that they feed on. *Patiriella vivipara* does not leave a mucus web behind it while feeding as reported for *P. exigua* (Branch & Branch, 1980). *Patiriella vivipara* does not feed upon macro-algae as does *A. gibbosa*. Macro-algae does not grow in the habitat of *P. vivipara*.

Patiriella vivipara is the largest and longest-lived of the three viviparous sea stars that have been investigated,

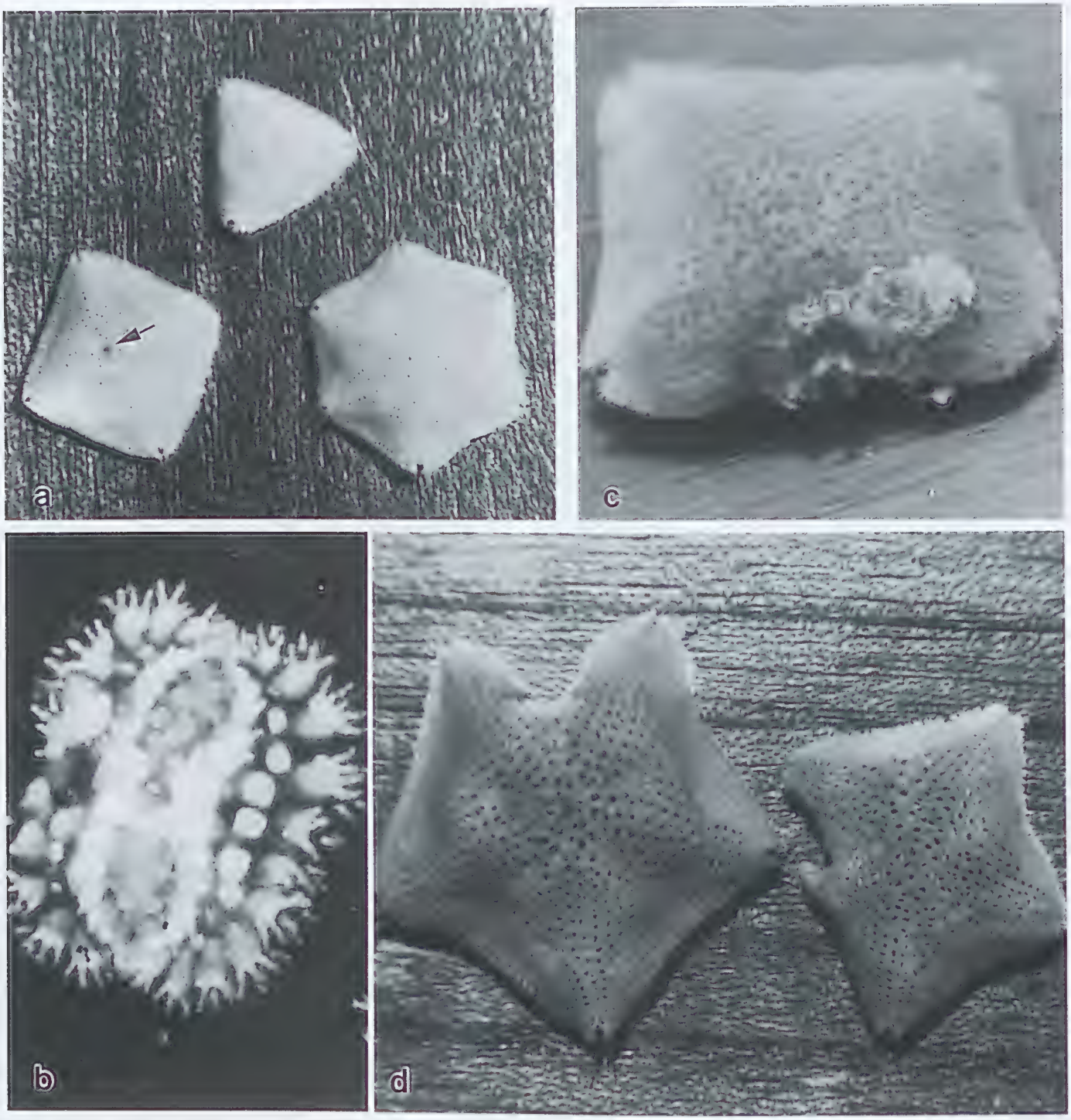

Figure 6. a, 3, 4 and 6 armed *Patiriella vivipara* raised in aquaria. The dark spot almost in the centre of the 4–arm specimen (arrow) is a small area of the "brown spot disease" (×2). **b**, The oral surface of the two-armed juvenile 5 months old, about 1 week before it died (×16). **c**, Necrosis caused by a severe attack of "brown spot disease". The sea star was affected interradially, and died about 2 weeks later (×4). **d**, Scars left by a non-fatal attack of the "brown spot disease" (×3).

attaining a maximum radius of 15 mm, and living for 8–10 years. In comparison *Asterina pseudoexigua pacifica* grows to a maximum radius of 10 mm R, and lives for 2–3 years (Komatsu, pers. comm.). *Patiriella parvivipara* is the smallest of these sea stars, growing to a maximum 4.70 mm R, and based on aquarium observations is suggested to live for approximately one year (Keough & Dartnall, 1978).

Although the main period for birth of juvenile *P. vivipara* appeared to be December to February, this was not consistent over the eight years of study. *Patiriella vivipara* is capable of reproducing throughout the year. In aquaria, an average of five juveniles per year were born to each adult, while the average in the quadrat was about two. The quadrat average may be an underestimation, as the sea stars in the quadrat were not restricted in their movement

as were the ones in the aquaria. Juvenile *P. vivipara* leave the parent at an advanced size, ranging in radius from 0.50–5.00 mm. Its smaller congener—*P. parvivipara*—which has a maximum radius of 5 mm, gives rise to juveniles of 2.00–2.50 mm diameter (Keough & Dartnall, 1978; Byrne, 1996). The largest newly emergent *P. vivipara* were 38% of the adults diameter, similar to that reported for *P. parvivipara*. In their first year after birth the juveniles exhibited a rapid growth rate in aquaria with a mean increase in radius of 2.85 mm. The first year of growth in *P. vivipara* is comparable to that recorded for *Asterina gibbosa* which increased in radius by 3.4–3.8 mm (Emson & Crump, 1978). *Patiriella parvivipara* gives birth to only a few juveniles in the summer months December to February, and the adult appears to die after the juveniles emerge. This species appears to live for only 12 months, thus the juvenile born one year becomes a parent the next year and has only has one season of reproduction (Keough & Dartnall, 1978).

In contrast to *P. vivipara, P. pseudoexigua* and *Asterina pseudoexigua pacifica* release a large number of small (R = 0.45 mm) young (Komatsu, *et al.*, 1990; Byrne, pers. comm.). *Asterina pseudoexigua pacifica* is capable of giving birth to 1000 or more juveniles in four weeks (Komatsu, *et al.*, 1990). At a radius of 0.45 mm, they are 4.5% of the adults diameter and are considerably smaller than newly released *P. vivipara* and *P. parvivipara*. The main period for development and birth of *A. pseudoexigua pacifica* is from mid-June to mid-July in the northern hemisphere summer (Komatsu, *et al.*, 1990). In Queensland, *P. pseudoexigua* releases young from September to November (Byrne, pers. comm.). At birth *A. pseudoexigua pacifica* and *P. pseudoexigua* have two pairs of tube feet, as do similarly sized juvenile *P. vivipara*. In comparison, *P. vivipara* emerge at a radius of up to 2.50 mm and with seven pairs of tube feet per arm. This advanced size is attained through intragonadal cannibalism (Byrne, 1996) and undoubtedly enhances their chance of survival. One year after birth *A. pseudoexigua pacifica* has six or seven pairs of tube feet per arm. *Patiriella vivipara* have 13–15 pairs of tube feet per arm at a radius of 7.00–8.00 mm one year after birth.

All four of these viviparous sea stars inhabit the intertidal zone. *Patiriella vivipara* usually occurs under rocks, and occasionally in rock pools. *Patiriella parvivipara* is found in rock pools, and as far as I can ascertain, *A. pseudoexigua pacifica* is also found under rocks. *Patiriella pseudoexigua* also occurs under rocks (Byrne, pers. comm.). Like *P. vivipara, P. parvivipara* and *P. exigua* experiences high summer temperatures, with the water in the pools reaching 30°C at low tide (Keough & Dartnall, 1978; Byrne, 1992). For *P. parvivipara*, tidal flushing made little difference to the temperature encountered by this sea star. *Patiriella vivipara* encounters a broad range of air temperatures, and for a relatively short period, water temperatures of up to 33°C while the tide initially comes in. Once the water reaches 0.3 m depth, the temperature starts to drop to whatever the deeper water temperature is at the time.

Since the initial surveys in the 1970's and 1980's, the populations of *P. vivipara* at Pittwater, Eagle Hawk Neck and Roches Beach have declined. Recent reconnaisance revealed that *P. vivipara* is not present along the Pittwater causeways in the numbers recorded in 1979. Several large colonies have almost disappeared from the south western shore of Upper Pittwater, and the remaining populations have decreased. The main population of *P. vivipara* at Pittwater is now found on the western shore of Midway Point.

Factors potentially influencing the decline of *P. vivipara* at Pittwater include the decrease in water quality associated with the discharge of effluent from sewerage treatment plants into Pittwater, seepage from areas serviced by septic tanks and from storm water runoff. The nutrients from these discharges can cause a heavy growth of epiphytes, and are thought to have contributed to the loss of sea-grass beds in Pittwater (Prestedge, 1996). Pittwater has experienced increased siltation since the early surveys and spaces between and under rocks previously occupied by *P. vivipara* have been filled by a combination of sediment and *Pyura stolonifera*. Storm water run off affects *Patiriella vivipara* populations located near drain outlets, and appears to cause a necrotic disease that kills some of the sea stars.

The population of *P. vivipara* on *The Tessellated Pavement* at Eagle Hawk Neck has decreased in association with the decline of the carpets of the small mussels *Brachidontes rostratus* and *Xenostrobus pulex* which they sheltered in. A drain carrying waste water has discharged just above the mussel zone for many years and may have contributed to the mussel die-off and the resulting decline of *P. vivipara*. In a survey conducted during February 1998, only 60 *P. vivipara* were found at this site.

The population of *P. vivipara* at Roches Beach has also decreased, but there is no obvious perturbation in the vicinity. A survey at this site during February 1998, the number of *P. vivipara* was estimated to be approximately 100.

The situation at Fortescue Bay is tenuous as the population is limited and the habitat does not appear suitable for an increase in the population of *P. vivipara*. At the present time there is very little pressure from human activity at this site.

In 1997 *P. vivipara* was found at Peppermint Bay, Woodbridge (Materia, pers. comm.). The presence of this species at this site appears to be due to release of adults from a nearby aquarium centre.

The decline in *P. vivipara* indicates that this sea star may be in danger of extinction. *Patiriella vivipara* was listed in July 1998 under the Tasmanian Threatened Species Protection Act, 1995, as follows: "*Patiriella vivipara* (viviparous seastar): Approved for listing on Schedule 3, Part 1—Endangered taxa of flora and fauna—Extant." Its limited distribution and low dispersive life history make it highly vulnerable to local perturbation. Considering its apparent decline since the original population census in 1976 and the scientific importance of this unusual species, some thought should be given to protection of *P. vivipara* and its habitat.

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A Giant New Trimerellide Brachiopod from the Wenlock (Early Silurian) of New South Wales, Australia

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ABSTRACT. *Keteiodoros bellense* n.gen. and n.sp. is a remarkably large trimerellide brachiopod from the Wenlock Dripstone Formation, southeast of Wellington, central New South Wales. The probable articulatory mechanism is unusual for trimerellides. It apparently involved both flattened sections of the lateral commissures which acted as pivots for opening and closing the shell, and a large and strongly modified articulating plate (which partly envelopes a robust dorsal umbo) articulating with the pseudointerarea at the posterior end of the ventral platform. The heavy dorsal umbo probably acted as a counterbalance to the anterior part of the valve; the diductor muscles were apparently acted as a counterbalance to the anterior part of the valve; the diductor muscles were apparently attached to the umbo at the sides of the articulating plate, and to the anterior end of the ventral platform.

The trimerellides occur in presumed life position in nearly monospecific beds which are interpreted as having formed in a quiet inshore shallow subtidal area on a sloping shelf, protected by coral biostromes but periodically disrupted by storm action. They are considered to represent a low-diversity quiet-water Benthic Assemblage 2 community.

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At a length of nearly 200 mm, the huge Silurian trimerellide brachiopod described herein as the new taxon *Keteiodoros bellense*, and a possibly ancestral genus in older (Ordovician) rocks about 70 km south of Mumbil, are amongst the largest known brachiopods. Trimerellides are a distinctive group formerly classified within the "Inarticulata", indicative of the fact that they supposedly lacked articulatory structures. Following recent re-evaluation of higher level brachiopod systematics, the trimerellides have now been moved to a position closer to

the old division "Articulata", based on their primitive, transitional hinging apparatus. The value of *Keteiodoros* is enhanced by its Wenlock age, since trimerellide brachiopods of that age are rare. Finally, it—and its probable Ordovician ancestor—provides useful insight into the functional morphology and phylogeny of the group, and the concomitant evolution of Palaeozoic shallow-water brachiopod communities

The brachiopod specimens were found in the core of the Oakdale Anticline northwest of Mumbil, in the Wellington district of central New South Wales (Fig. 1). The Mumbil area was first mapped in any detail by Strusz (1960); the anticline received closer attention from Vandyke (1970, unpublished), whose geological results were published by Vandyke & Byrnes (1976). Vandyke & Byrnes noted the presence of trimerellide banks at several localities in their Catombal Park Formation (now Bell River Member, Dripstone Formation, of probable late Wenlock age); the species was briefly described by Vandyke (now Byrnes) in her unpublished thesis.

Stratigraphy

The Bell River Member is the upper member in the Dripstone Formation (see Colquhoun *et al.*, 1997), and is overlain by the Narragal Limestone (Fig. 1). It reaches a maximum thickness of about 120 m, and comprises mostly acid volcanics, with subordinate shale and silty limestone (best developed at the base). A discontinuous dirty limestone at this level is partly biostromal, with an abundant fauna of rugose and tabulate corals and stromatoporoids, some in life position, and rare other taxa, including the trilobite *Pacificurus* (formerly a subgenus of *Encrinurus*, and placed in synonymy with *Batocara* by Holloway, 1994, a move with which Strusz disagrees). The coral fauna was described by Strusz (1961), with revisions of the rugosans by McLean (1975), and some of the tabulates by Webby & Semeniuk (1969). The dominant rugosan is *Palaeophyllum oakdalensis*, associated with which are *Aphyllum lonsdalei, Holmophyllum struszi* and *Holmophyllia maculosa*; the tabulates include *Propora conferta, Multisolenia tortuosa, Favosites gothlandicus, Acanthohalysites australis, Falsicatenipora bellensis* and *F. chillagoensis*. The taxonomic positions of the various taxa (whose authorship can be found in the above-mentioned papers) have been updated in Strusz (1996). Vandyke & Byrnes (1976) listed some of the coral localities in Strusz (1961) which they considered to lie within the "Catombal Park Formation". From data held by Strusz, those should include S71, S122, S208, and S285 (see Fig. 1); the collection from S65, at the base of a steep ridge, may be a mixed fauna, including specimens derived from the younger Narragal Limestone higher on that ridge.

Age

Largely on the regional relationships of the faunal association characterised by that of the Dripstone Formation, Vandyke & Byrnes (1976) argued for a late Wenlock or, less probably, early Ludlow age. Although no new information has been obtained on the age of the Bell River Member, diagnostic conodonts have recently been recovered from the base of the overlying shallow-water Narragal Limestone, as well as from outcrops of probable Wylinga Member (basal Dripstone Formation) within an infaulted sliver to the west of the Oakdale Anticline.

New South Wales Geological Survey conodont sample C1430, from the basal Narragal Formation, contains *Coryssognathus dubius* (Rhodes, 1953). In the British succession (Miller & Aldridge 1993) this species extends through strata of latest Gorstian and Ludfordian age (i.e. upper Ludlow). In northeastern Victoria Simpson & Talent (1995) found it in strata ranging from possibly latest Wenlock (but no older) to Ludlow. At Yass, N.S.W. (Link & Druce 1972; stratigraphic terminology following Owen & Wyborn, 1979), *Coryssognathus dubius* is sparingly represented in the Cliftonwood Limestone Member (Yass Formation), Euralie Limestone Member (Laidlaw Formation), and Hume Limestone Member (uppermost Silverdale Formation). According to Simpson (1995), the range at Yass may start in the Wenlock and extends into the *siluricus* Zone (early Ludfordian) of the late Ludlow. Therefore, while the base of the Narragal Limestone may be as old as Wenlock, the majority of this formation is of Ludlow age. The overlying Barnby Hills Shale (see Fig. 1) contains an horizon with abundant *Bohemograptus*, suggesting for it a Gorstian-Ludfordian age; Rickards & Wright (1997) suggested correlation with the *B. kozlowskii* Biozone (Ludfordian) for this graptolite fauna. The Barnby Hills Shale is overlain by the Cuga Burga Volcanics which, nearer Wellington, also overlie the Camelford Limestone. The latter unit straddles the Silurian/Devonian boundary (Chatterton *et al.*, 1979).

The probable Wylinga Member conodont sample (C1453) contains *Ozarkodina excavata eosilurica*, which ranges through the *celloni* and *amorphognathoides* Zones, of Telychian (late Llandovery) to early Wenlock age.

Thus the Bell River Member, which succeeds the Wylinga Member and overlying Warderie Volcanics, and is itself overlain disconformably by the Narragal Limestone, is almost certainly Wenlock, and most probably Homerian in age.

Occurrence and environment

Keteiodoros bellense is known from three localities, S122, S285 and S208 (Fig. 1), in a silty limestone within the shaly basal part of the Bell River Member. The best exposures are at and near S285, where several *in situ* shell banks are developed, interspersed with biostromes of *Palaeophyllum oakdalensis*. The majority of the shells are oriented umbo-down, with the valves conjoined, resting in life position (Fig. 2). The sediment below the lowest bank is brown siltstone, apparently devoid of fauna. Thin sections of the silty carbonate rock surrounding the beak of one in-situ specimen (Fig. 3) show it to be an orange-brown skeletal wackestone, with shelly debris distributed in terrigenous mud; algae are present. Field observation shows that the enclosing sediment contains a few

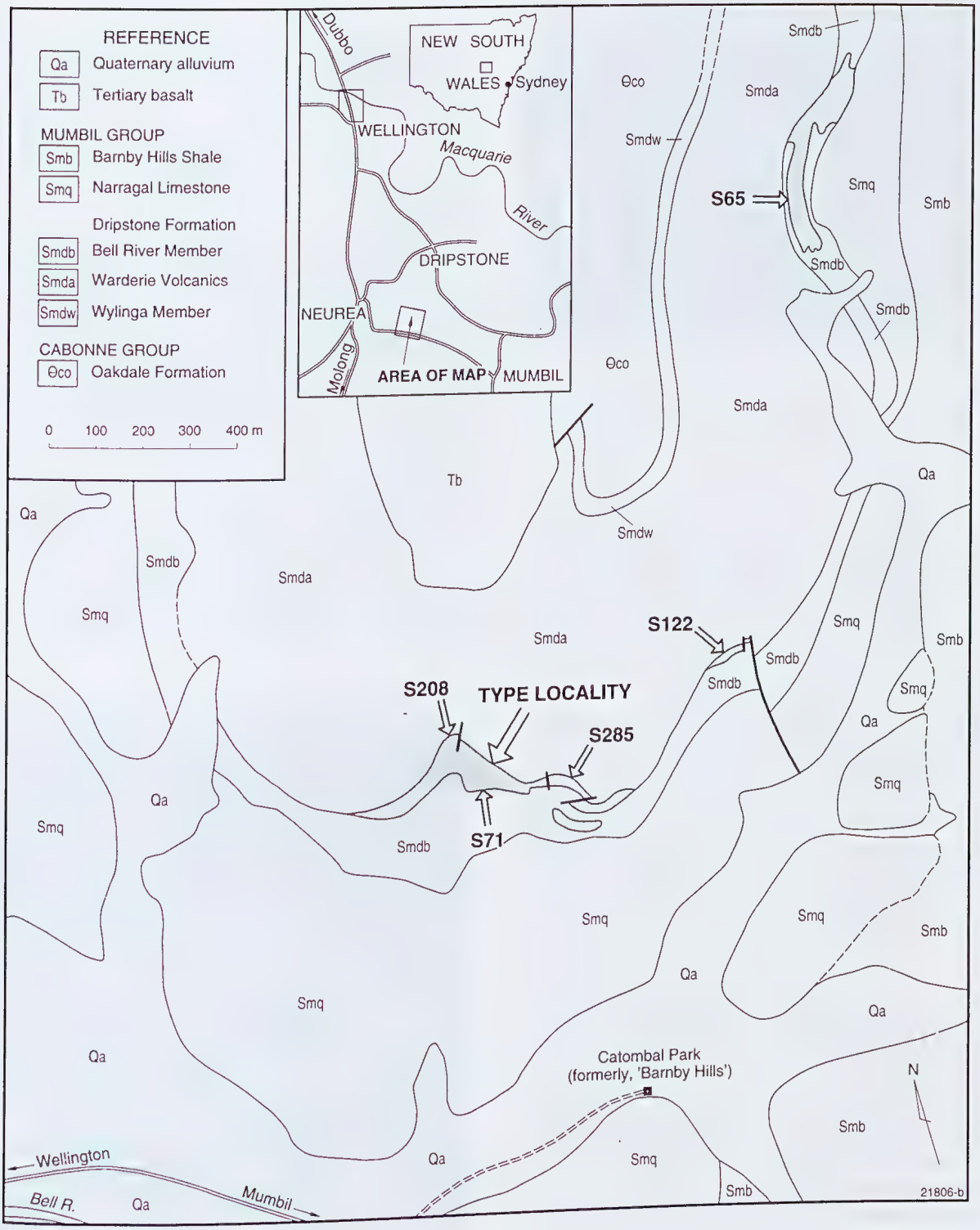

Figure 1. Geological map of the Oakdale Anticline (Mumbil district), showing also the position of Strusz's (1960) localities in the Bell River Member, Dripstone Formation. The basal shaly-calcareous part of the Member is stippled; the shells described herein come from the arrowed area between localities S285 and S208. Modified after Vandyke & Byrnes (1976). Grid references for the three trimerellide localities (Wellington 1:50,000 sheet 8632 I+IV) are: S122—687300E, 6381550N; S208—686950E, 6381250N; S285—687100E, 6381350N.

disoriented shells, mostly relatively small, and many of the larger shells have damaged anterior ends. The shells show no sign of attachment structures, and, especially given the degree of posterior overlap of the valves in mature shells, there is no evidence that they could have had pedicles. The sediment was therefore the probable supporting medium for the generally fairly closely aggregated shells (compare Webby & Percival, 1983, and Pollock, *et al.*, 1994). The presence of algae is reminiscent of the occurrence of *Hedstroemia* in association with *Eodinobolus* shell beds at Fossil Hill, near Cliefden Caves. Webby & Percival (1983) interpreted these algal mats as

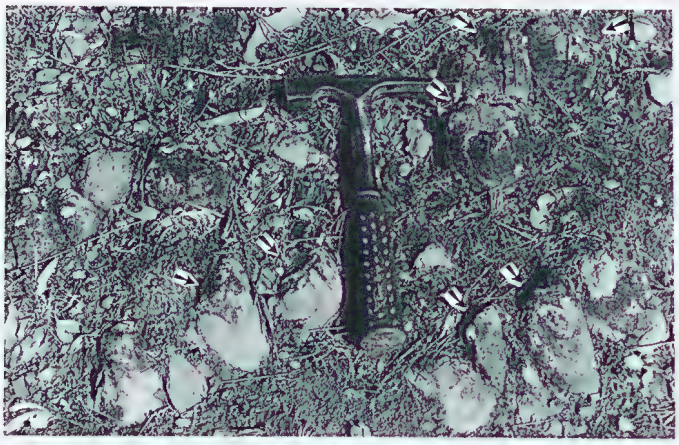

Figure 2. Outcrop photo of several successive shell layers below the main *Palaeophyllum* biostrome; arrowed are shells clearly in life position (umbo down), with truncated upper ends.

providing a temporary stable surface on a mud substrate, permitting settling of larval trimerellides. While the algae observed in the Bell River Member are not mat-like, but rather are vertically-radiating in growth form, they could still have acted as initial attachment points above the substrate.

It seems likely that the environment was lagoonal, subject to occasional storm disturbance. For the thickest shell bed this is strongly indicated by the orientation of the shells in life position, and the destruction of their anterior (i.e. upper) ends at distinct levels within the bed. Many of the damaged shells have large shell fragments (including parts of juvenile shells) within their mud-filled body cavities, indicating severe turbulence. At least one level of disturbed and randomly oriented adult shells is present near locality S285, immediately overlain by a monospecific *Palaeophyllum* biostrome. Between this biostrome and another approximately 8–10 cm above it lies an horizon of *in situ* juvenile shells. This we interpret as an attempt to recolonise the substrate by the *Keteiodoros* community, which was then catastrophically destroyed by another storm, probably smothering the juveniles with sediment before they grew to maturity. There thus appears to have been a consistent vertical (and possibly lateral) depth relationship in the Bell River Member between *Keteiodoros* and *Palaeophyllum*, with biostromes of the latter overlying banks of the former. The biostromes show every evidence of an energetic environment, in contrast to the shell banks which represent a quieter one disrupted periodically by storms. This suggests to us that the shell banks were in shallow water, possibly lagoonal, normally protected by the corals (perhaps forming a wave barrier offshore from a volcanic island), and not in an open shelf environment. The regional geology precludes the possibility of gently sloping open shelf areas with significant basinward extent.

These large shells must have been relatively heavy, since the walls are posteriorly very thick and the umbonal regions solid. It is likely that the posterior third of a large shell would have been buried in the generally fine sediment, thus imparting considerable stability. Their size and robustness makes it tempting to compare these trimerellides with the massive bivalve *Eurydesma cordatum*, the ecology of which was described by Runnegar (1979). Runnegar deduced that when disinterred from its normal semi-infaunal position the equivalved *Eurydesma* was able to maintain its upright orientation in an active water environment in the manner of a roly-poly toy. *Keteiodoros*, however, has strongly asymmetrical valves and a protruding ventral beak, so that, unlike *Eurydesma*, reorientation would not have been possible. Thus while both shells lived partly buried in the substrate to a similar relative depth, and similarly developed a low centre of gravity enhanced by grossly thickened umbonal regions for stabilisation, *Eurydesma* was adapted to turbulent water and a resulting coarse-grained substrate, whereas *Keteiodoros* could only colonise quiet environments with a muddy substrate. The trimerellide presumably used its weight, and a degree of mutual crowding, to remain stable while keeping the anterior part of the shell above the sediment surface, so avoiding sediment-fouling of the body cavity (compare *Eodinobolus* as discussed in Webby & Percival, 1983). The biotic diversity of the *Eurydesma* community appears to be much higher than the nearly

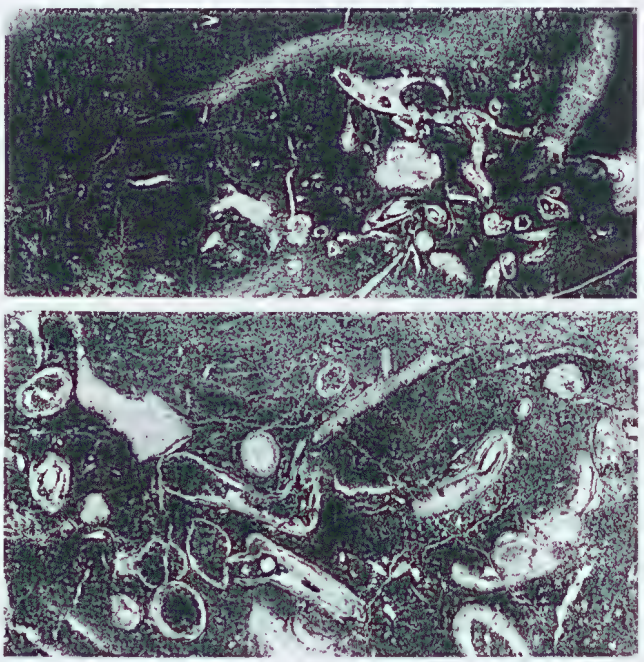

Figure 3. **A–B**—thin sections of the rock surrounding the beak of in-situ paratype MMF 33364; **A**—slide MMF 33364b; **B**—slide MMF 33364a, both scale bars 5 mm. The rock is an orange-brown skeletal wackestone, the matrix being terrigenous mud incorporating shelly debris, including ostracods (B). There are also pockets of coarser debris, usually 1–10 mm across but up to 25 mm; components include disarticulated juvenile *Keteiodoros* (A, top centre), the tabulate coral *Syringopora*, the stromatoporoid *Ecclimadictyon*, a fine stenoporoid bryozoan, three different algae (including a solenoporacean and *Ortonella?*), and rare gastropod and echinoderm fragments. The fragments show little sign of erosion, suggesting they have not been moved far.

monospecific *Keteiodoros* beds. A final difference is that *Eurydesma* was a high-latitude cold-water species, while in the Silurian the Lachlan Fold Belt was in subtropical to tropical latitudes (Walley *et al.*, 1990).

Benthic Assemblage position

In terms of the level-bottom Benthic Assemblages of Boucot (1975), the Trimerelloid Community Group of Wang *et al.* (1987) is usually considered to be a low-diversity high-energy B.A. 3 group of communities, and this was followed by Strusz & Garratt in Boucot & Lawson (in press) for the Catombal Park occurrences. The more detailed evidence cited above, and also that from Late Ordovician trimerellide shell banks documented from central N.S.W. by Webby & Percival (1983), suggests that more inshore (and hence, shallower water) habitats flanking volcanic islands were also preferentially colonised by these brachiopods. Indeed, Percival & Webby (1996) interpreted the *Eodinobolus* biofacies of the Molong High to have occupied a restricted marine (most likely lagoonal or protected embayment) setting equivalent to a B.A. 1 or upper B.A. 2 position, i.e. intertidal to very shallow subtidal. The environment inhabited by the nearly contemporaneous rotund trimerellide *Belubula* was also interpreted as lagoonal (Percival, 1995). Normal open-shelf shallow-water B.A. 1 & 2 environments are above wave base, while B.A. 3 is within the photic zone but subtidal, below normal wave base. However, in protected shallow water habitats such as lagoons, normal wave activity is of less consequence to the marine benthos than are tidal currents and, in particular, storms, and the normal depth connotations are difficult to apply. The difficulties in relating low-diversity low-energy B.A. 2 communities to normal B.A. 2 and B.A. 3 communities have already been discussed by Boucot (1975: 34–36). As noted above, *Keteiodoros* lived in such a quiet environment, but subject to storm damage (apparent even in thick gerontic shells of *Keteiodoros*, the anterior ends of which are typically eroded, or, in some complete specimens, stove in—see Fig. 2). In conclusion, we assign the *Keteiodoros* shell beds to a quiet-water B.A. 2 position, inshore of a protective *Palaeophyllum* wave barrier—thus different from the low-diversity high-energy B.A. 3 Trimerelloid Community as defined by Boucot (1975—who did note on p. 236 that more ecologically-oriented study may reveal greater complexity). It may be significant that in two of the three Molong High occurrences noted here (of *Belubula* and *Keteiodoros*), the trimerellides are larger and far more rotund than those found in the B.A. 3 Community, while the third comprises a moderately rotund but very large *Eodinobolus*. *Adensu* may occur in a quiet-water B.A. 2 setting, but the information provided by Popov & Rukavishnikova (1986), while recalling the *Keteiodoros* situation in some respects, is not detailed enough for a positive conclusion.

Preparation techniques

The information on which the description and analysis of *Keteiodoros bellense* are based has been obtained in several ways, because none of the specimens is sufficiently well preserved to provide all the data. The interiors of two apparently suitable specimens were mechanically prepared, but when that task (made very difficult because the matrix is no softer than the shell) was well advanced it became clear that there were problems in the umbonal area, and so a specimen was serially sectioned, and acetate peels made. Recrystallisation made these acetate peels difficult to interpret (compare Fig. 8), even when the surfaces were stained with Alizarin Red. In the end, the polished and etched surfaces were covered with abutting wide strips of "Magic tape", and the structures traced on this in pencil under the microscope. This done, even wider strips of clear polyester tape were laid across the "Magic tape", and the tracings lifted and transferred to clean paper. Xerographic copies of each traced surface were checked against the original surfaces under the microscope to make sure no preservational artefacts had been wrongly interpreted as structures, and corrected drawings were then prepared on a light table. A reconstruction of the interior was prepared from these. To check the interpretation of several problematic structures, other specimens were cut as close to the median plane of symmetry as possible, or at right angles to it, and polished. Finally, one of us (IGP) found a few silicified specimens on a subsequent visit to the locality, and careful etching (and reinforcing of the very fragile fragments) revealed hitherto undetected structures and internal relationships. No one method had provided sufficient information; put together, they have, we believe, given us a clear picture of this unusual brachiopod.

Systematic description

We adopt the supra-familial classification proposed by Popov *et al.* (1993) as modified by Williams *et al.* (1996). Terminology and generic authorship follow the Treatise on Invertebrate Paleontology, Part H (Williams & Rowell in Williams *et al.*, 1965) unless otherwise noted. Type material is lodged with the Australian Museum (registration acronym AM F) in Sydney, the Commonwealth Palaeontological Collection (CPC) maintained by the Australian Geological Survey Organisation in Canberra, and the New South Wales Department of Mineral Resources Palaeontological Collection (MMF), Mineral Resources Development Laboratory, Lidcombe, Sydney. Additional material is held by those organisations and the School of Geosciences, University of Wollongong.

Subphylum **Craniiformea**
Popov, Bassett, Holmer & Laurie, 1993

Class **Craniata**
Williams, Carlson, Brunton, Holmer & Popov, 1996

Order **Trimerellida**
Goryansky & Popov, 1985

Superfamily **Trimerelloidea**
Davidson & King, 1872

Family **Trimerellidae**
Davidson & King, 1872

Keteiodoros n.gen.

Type species. *Keteiodoros bellense* n.sp. Wenlock, New South Wales. No other species are presently known.

Derivation of name. Greek κητειος = sea-monstrous + δορός = leather bag; neuter gender. The name is an allusion to original environment, size, and resemblance to an ovoid football.

Diagnosis. Very large and strongly equibiconvex trimerellide brachiopod, each valve with deeply excavated steep-sided platform supported by long median septum; deep umbonal cavities in ventral valve; ventral umbo long, incurved; dorsal umbo strongly incurved, bulbous, fitting against posterior end of ventral platform; long thick longitudinally and transversely curved articulating plate more or less concentric with umbo, extending from dorsal beak almost to surface of ventral platform; valve margins slightly overlapping dorsoventrally in front of flattened zones which served as articulation pivots.

Discussion. Because of the unusual morphology of this form, discussion of its relationships follows the specific description.

Keteiodoros bellense n.sp.

Figs. 4–13, Table 1

Type material. HOLOTYPE: AM F101116, a partly prepared incomplete shell (Fig. 7A). PARATYPES: AM F101117–101128, 101133–101135, CPC 34408–34416, MMF 30558, 33364–33367.

Other material. AM F101129–101132, 101136–101147, CPC 34417–34419, MMF 30557, 30559, 33368–33370.

Type locality. Between localities S208 and S285 of Strusz (1961), above the head of a small gully within the Oakdale Anticline about 750 m north-northwest of "Catombal Park" (formerly "Barnby Hills") homestead, Parish of Mumbil southeast of Wellington, New South Wales (extended grid reference 686970E, 6381300N, Wellington 1:50,000 sheet 8632 I+IV). See Fig. 1.

Type horizon, age. Low in the Bell River Member, Dripstone Formation, Mumbil Group. Homerian?, late Wenlock, Early Silurian.

Diagnosis. As for genus.

Description. *External morphology*: The shell is large, globose, thick-walled, approximately equibiconvex; smooth apart from growth lines (Fig. 5A). The only well-preserved complete shell of the very few known (paratype AM F101117, Fig. 4) has its greatest depth at mid-length, greatest width at about ¾ length (see Table 1 for dimensions). Other relatively little-damaged shells suggest the greatest depth is often further forward. In cross section the shell is ovoid, generally deeper than wide. The commissure is sinuous laterally, and anteriorly shows a broad shallow dorsally-directed tongue. The ventral valve is medially flattened for most of its length, the flattened zone changing to a broad sulcus near the anterior margin. The dorsal valve is also boat-shaped in cross-section: gently curved laterally and medially, strongly curved in between. The ventral umbo is long, rather flattened, pointed, anacline, and suberect to strongly incurved (Figs. 4, 5). No specimen is well enough preserved to show the inner surface of the beak, while transverse sections (Fig. 6) and one silicified fragment (MMF 33367) are equivocal, so the presence of a pseudointerarea cannot be firmly established, but we interpret the area on the ventral valve posterior to the dorsal umbo and more or less continuous with the ventral platform as a poorly defined pseudointerarea. There is no sign of a homeodeltidium. The dorsal umbo is deeply incurved, strongly swollen, and generally concealed beneath the ventral beak; its ventral surface matches the transverse profile of the pseudointerarea where the two are in contact (see Figs. 6, 7). Dark lines in longitudinal sections, probably indicating the buried surface of the dorsal platform, show a spiral trace through as much as 300°. One of the silicified paratypes (MMF 33365, Fig. 9) reveals a sharply pointed beak with an apical angle of 110°; the beak is also markedly asymmetric, being directed right-ventrolaterally at about 60° to the commissure. Similar but much weaker asymmetry is also apparent in another silicified paratype (MMF 33366, Fig. 10).

Posterior to about 20% of total length (about 55 mm in the sectioned shell, Fig. 6), the margins of the dorsal valve are broadly rounded, and lie within the ventral valve, merging posteriorly with the swollen dorsal umbo. Somewhat forward of that level (at about 60 mm in Fig. 6) they become thinner, and rest against the outer edge of the ventral valve margin. Where the dorsal valve margins change from being inside to outside the ventral valve margins, there are short transitional zones where both margins have thick flattened tops which we interpret as pivot surfaces for valve movement (55–58 mm in the sectioned shell, and apparent in paratypes CPC 34410, Fig. 7B, and MMF 33364, Fig. 8). Forward from there (60–75

Figure 4. **A–E**—the only well preserved nearly complete (although somewhat worn) shell, paratype AM F101117. **A**—dorsal view; **B–E**—lateral, ventral, anterior and posterior views (dorsal valve uppermost in D and E); 2 cm scale bars. The anterior edges of the valves are slightly damaged (E); the rapid development of the ventral sulcus near the anterior margin is clearly visible in C and E, while B shows the relationship of the valve margins behind and in front of the pivot zone.

mm), a low flange develops on the inner edge of each ventral valve margin which fits into a groove near the inner edge of each dorsal valve margin. The inner edges of the grooves disappear forwards, leaving the tapered outer edges of the dorsal valve margins resting against the outer surfaces of the ventral flanges. The flanges in turn become lower, the ventral valve margins narrow, and from about the shell mid-length the commissure assumes a more conventional appearance, without any overlap of dorsal valve over ventral valve.

Ventral interior: The ventral platform is strongly developed, about 40% as high as the valve and occupying about a third of the total width anteriorly. It extends well beyond mid-length, and covers a large cavity which is divided into two long vaults by an even longer median septum which may reach the start of the anteroventral sulcus. In cross-section the sides are steep to slightly overhanging, and gently convex, while the upper surface is a broad shallow trough which longitudinal sections and the excavated shell show is not a continuous smooth curve

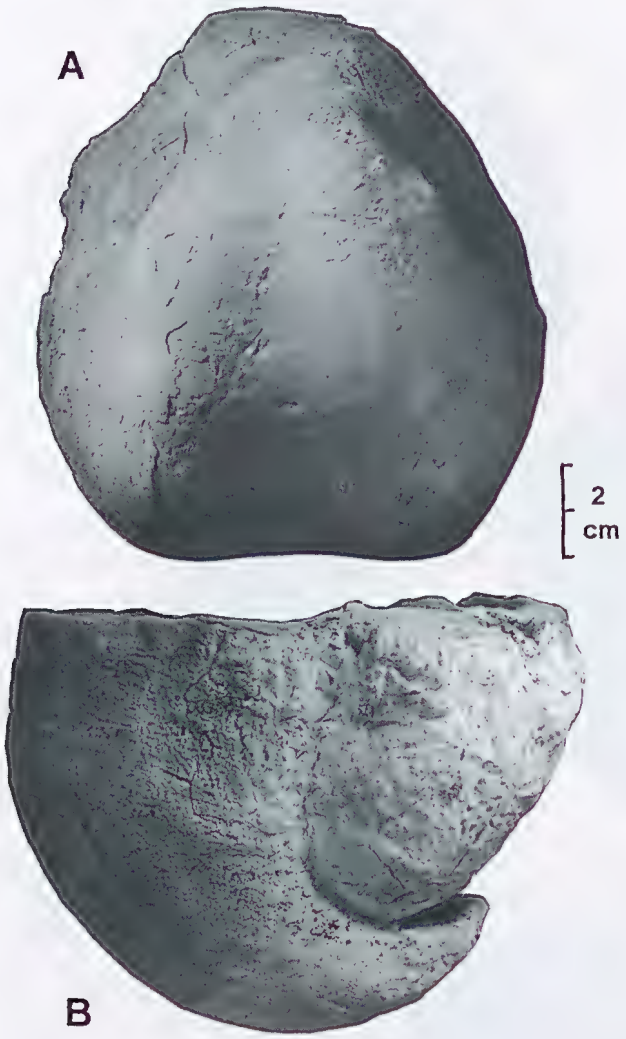

Figure 5. Incomplete large shell, paratype CPC 34408; 2 cm scale bar. The exterior of the ventral valve displays growth lines where adhering sediment has been mechanically removed, and anteriorly a broad very shallow sulcus. The side view shows the shell in inferred life position; the preserved part of the shell was probably below the sediment-water interface, and so protected from storm damage by the surrounding sediment. The restricted space between ventral and dorsal umbos is evidence for the severe limit imposed on the angle of gape.

in front of the contact zone with the dorsal umbo, but terraced, the faces of the terraces facing forward. The one silicified ventral valve fragment (MMF 33367) shows a strong but fairly smooth bulge in a position just forward of where the remnant of the dorsal umbo rests against the pseudointerarea Posteriorly, the upper edges of the platform rise steeply and flare outwards then forwards to merge with the valve margins in continuity with (and so buttressing) the marginal flanges which interlock with the dorsal valve. They thus enclose deep umbonal cavities whose apices are about level with or slightly behind the flattened pivot surfaces on the valve margins (Fig. 6). The platform vaults are increasingly constricted posteriorly by thickening of the top and sides of the platform; from the sections, the vaults start in front of the umbonal cavities. There is also a narrow and relatively short conical cavity at the junction of the platform and median septum. No muscle impressions have been seen on the available specimens.

Dorsal interior: The dorsal platform is similar in extent and form to that in the ventral valve, including a strong median septum and long vaults, but its edges merge posteriorly with the swollen beak rather than with the valve margins. The platform surface appears to be smooth, without any indication of muscle insertion. Umbonal cavities are apparently absent but, as with the ventral platform, there is a narrow cavity at the front of the platform, at its junction with the median septum. There is a close fit between the dorsal umbo and the posteriorly raised margins of the pseudointerarea (Figs. 5, 6). Partly enveloping the dorsal beak is a thick curved plate (see Fig. 8), which arises from a large mass of dense tissue resting on the posterior end of the dorsal platform. This plate is concentric with, but raised above, the dorsal umbo, and extends longitudinally through an arc of about 120 to 150°, such that it approaches the surface of the ventral platform. In paratype MMF 33366 its base is supported by a distinct ridge extending straight up from the surface of the platform; this, presumably the cardinal buttress, is not evident in the transverse sections. Silicified paratypes MMF 33365 and 33366 (Figs. 9, 10) show that the laterally placed recesses between plate and umbo are striated; they are presumed to have been sites of diductor muscle attachment (see discussion below). Longitudinal sections (Fig. 11) show that the distal end of the articulating plate faces a terrace on the ventral platform. Beneath that terrace distinct closely

Table 1. Dimensions in millimetres of selected shells; dimensions are approximate, with those in brackets estimated on the basis of predicted complete outline.

		length	width	depth
Holotype	AM F101116	(180)	>110	130
Paratype	AM F101117	145	115	125
Paratype	AM F101128	(135)	101	112
Paratype	AM F101133	(139)	108	116
	AM F101142	144	>85	>105
Paratype	CPC 34408	(180)	>120	130
Paratype	CPC 34409	(135)	95	85
Paratype	CPC 34411	(170)	120	135
Paratype	CPC 34412	(160)	>145	120
Paratype	MMF 30558	>130	105	120
Paratype	MMF 33364	126	127	
	MMF 30557	>102	123	122
	MMF 30559	>140	118	(125)
	MMF 33368	>160		
	MMF 33369	>135		>84
	MMF 33370	>98	>82	(75)

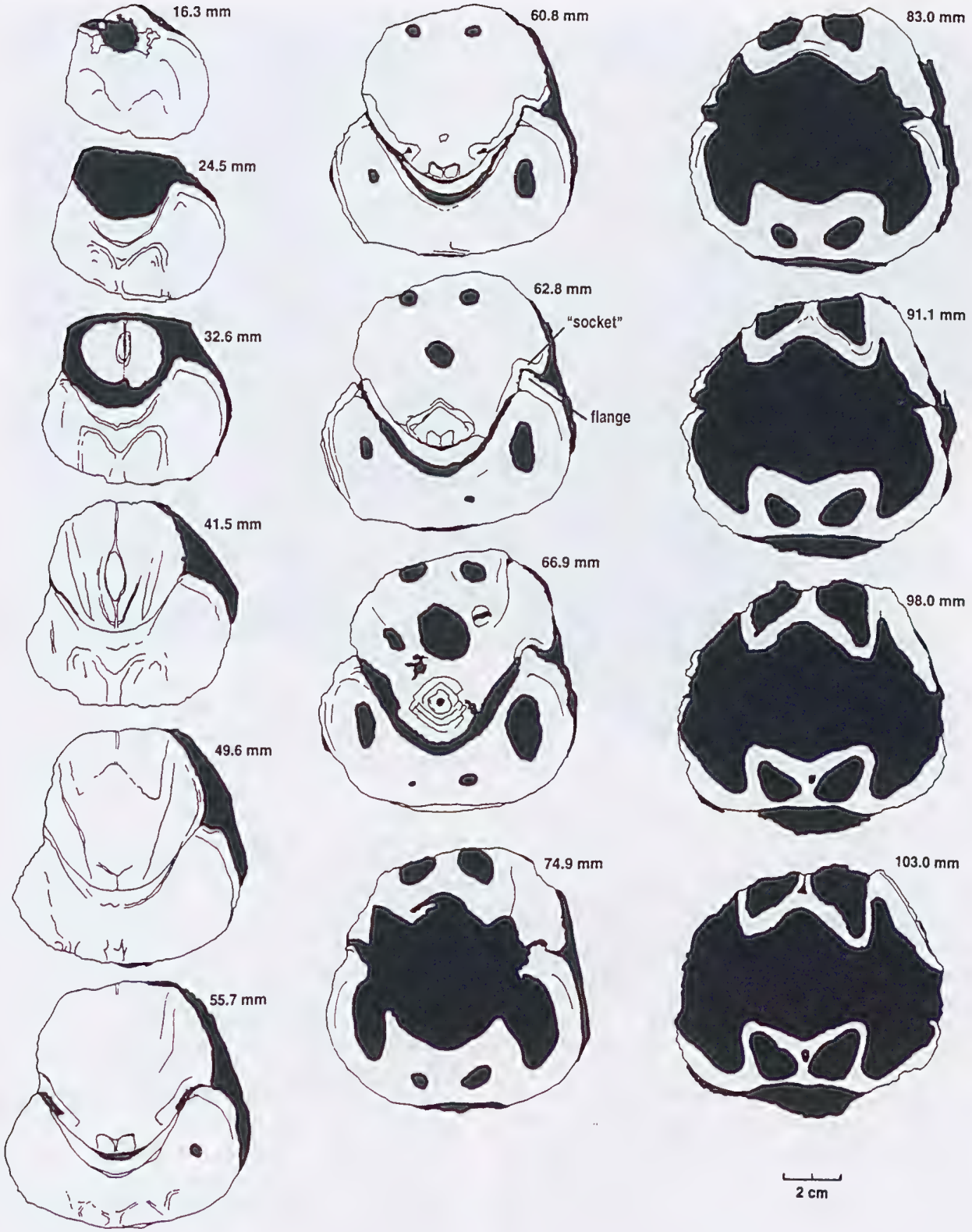

Figure 6. Selected serial sections of a nearly complete shell, paratype CPC 34409; distances are from the ventral umbo, parallel to the plane of commissure, and black areas are adhering or infilling sediment; 2 cm scale bar at lower right. The last section with traces of shell was at 157 mm, and the reconstructed longitudinal profile (see Fig. 13) suggests this was close to the relatively abrupt anterior closure of the shell. The interlocking flange-"socket" arrangement in front of the pivot zones on the valve margins is labelled on the 62.8 mm section.

spaced growth traces can be seen, and the tissue here is clearly a pad resting on the surface of the ventral platform, rather than being part of the platform structure itself; it probably corresponds to the swelling seen in MMF 33367.

Dimensions (Table 1). There are only one or two more or less complete shells, all others being damaged. In most cases only the posterior half (more or less) of the shell is preserved, and examination of the outcrop reveals that this is a function of the living position. The shells occur in

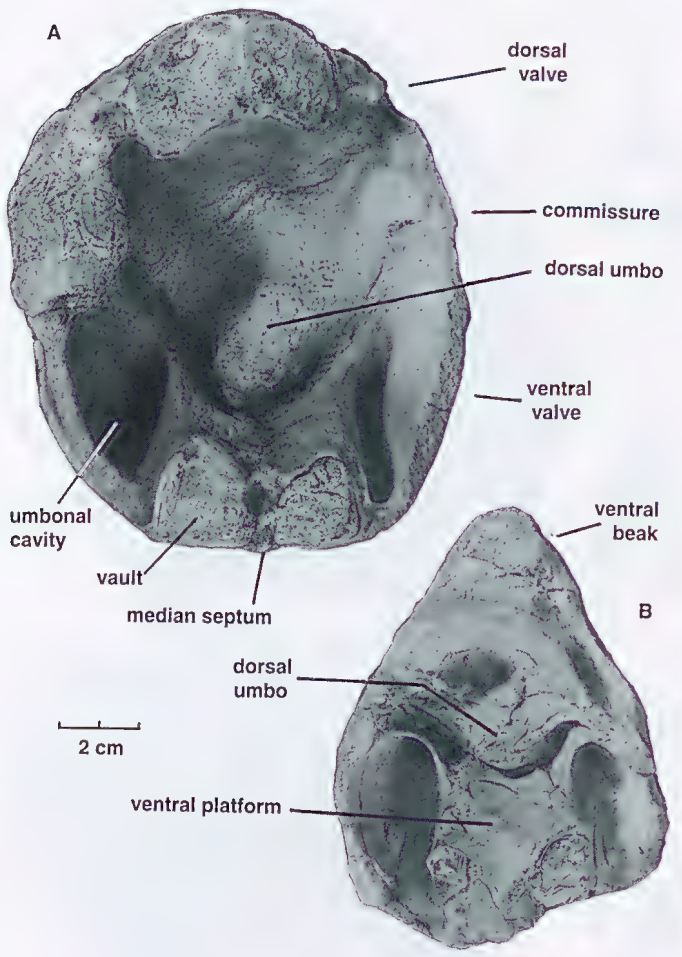

Figure 7. **A–B**–two prepared incomplete shells; 2 cm scale bar at lower left. **A**—holotype AM F101116 in anterior view; the vaults on both valves have not been cleaned out, and there is still some sediment at top left adhering to one side of the dorsal valve; the dorsal umbo has been partly removed during preparation, as it was difficult to distinguish recrystallised matrix from recrystallised shell, and such a large umbo was not expected in that position. **B**—paratype CPC 34410 in anterodorsal aspect, a partly prepared incomplete ventral valve with part of the dorsal umbo still resting on the ventral platform.

relatively crowded layers, mostly beak downwards, and each layer has been truncated by storm action, removing or damaging the anterior ends of the larger shells. In many shells the valves are gaped and slightly dislocated. The originally probably aragonitic shells are recrystallised (at times very coarsely—see Figs. 8, 11) to calcite, and weathered-free shells have generally lost part or more often all of the outer surface. Consequently in most cases the dimensions for width and depth shown in Table 1 are approximate, and for length or depth an estimate using the one complete shell provides a guide to probable outline.

Discussion. Few described trimerellides approach *Keteiodoros bellense* n.sp. in size or convexity. Closest are the gigantic *Belubula* Percival, 1995, from the Upper Ordovician Belubula Limestone southwest of Orange, NSW, and the somewhat smaller *Adensu* Popov & Rukarishnikova, 1986, from rocks of similar age in southern Kazakhstan. *Belubula*, estimated to have reached a length of 20 cm, is also comparable with *Keteiodoros* in its deep ventral umbonal cavities, but the ventral platform is low, not vaulted or excavated, and there is a stout cardinal buttress; the dorsal platform, too, is relatively low. At a length of about 90 mm and a depth of 50 to 70 mm, *Adensu* is only half the maximum size of the Australian shells. The genus was made the type of a new trimerellide family based partly on large size and great convexity, but mainly in having raised dorsal muscle fields separated by deep grooves, and lacking the typical trimerellide platforms in both valves. Percival (1995) did not think the available material justified a separate family, and pointed out similarities with gerontic *Eodinobolus stevensi* Percival, 1995, from the Fossil Hill Limestone.

While *Trimerella* and *Dinobolus* have vaulted platforms in both valves, their shells are much less convex, the ventral beaks are high and not strongly incurved, with well differentiated pseudointerareas, and the dorsal umbos are small. In all these features they are unlike *Keteiodoros*. Articulation in *Trimerella* is obscure but, in *Dinobolus, Eodinobolus* and *Gasconsia*, and possibly *Monomerella* and *Adensu*, it appears to comprise a transverse cardinal socket overhanging the platform in the ventral valve, in which rests the posterior edge of an articulating plate which is effectively the thickened and protruding posterior margin of the dorsal valve (Norford, 1960; Norford & Steele, 1969; Hanken & Harper, 1985; Popov & Rukavishnikova, 1986; precise details of the articulation have been questioned by Mergl, 1989). The simpler term "hinge plate" is already used for part of the cardinalia in rhynchonellate brachiopods. The arrangement in *Keteiodoros* is seemingly more complex: it uses areas on the valve margins as pivoting surfaces, while medially there is articulation between the ventral surface of the dorsal umbo on the one hand, and the surface of the pseudointerarea on the other, a little like a unidirectional "ball and socket" joint; the articulating plate appears to have served mainly as a "stop" to unwanted longitudinal movement, and as a protective cover for the diductor muscle attachment.

Possibly related is *Monomerella ovata* Whiteaves, 1884, from the Ludlow-age Guelph Dolomite of Ontario (Holmer, pers. comm., 1997). Dorsal internal structures, critical to generic assignment, have not been described, but the ventral interior illustrated by Hall & Clarke (1892, pl. IVD, fig. 15) differs in its long well-differentiated pseudointerarea and much shorter platform. In Australia, Talent (pers. comm., 1995) has collected rather smaller but externally very similar specimens from the Wenlock-Ludlow Yarrangobilly Limestone in New South Wales, and the Silurian at Chillagoe in northern Queensland; these remain undescribed.

Finally, it is interesting to compare the quite specialised *Keteiodoros*, with its complex morphology and gigantic size, with *Ussunia* Nikitin & Popov, 1984, from the late Llandeilo to early Caradoc of Kazakhstan. An early trimerellide-like genus displaying features transitional from craniopsids, *Ussunia* is biconvex but not at all globose, with an undifferentiated pseudointerarea extended anteriorly as a flattened limbus. Muscles were inserted

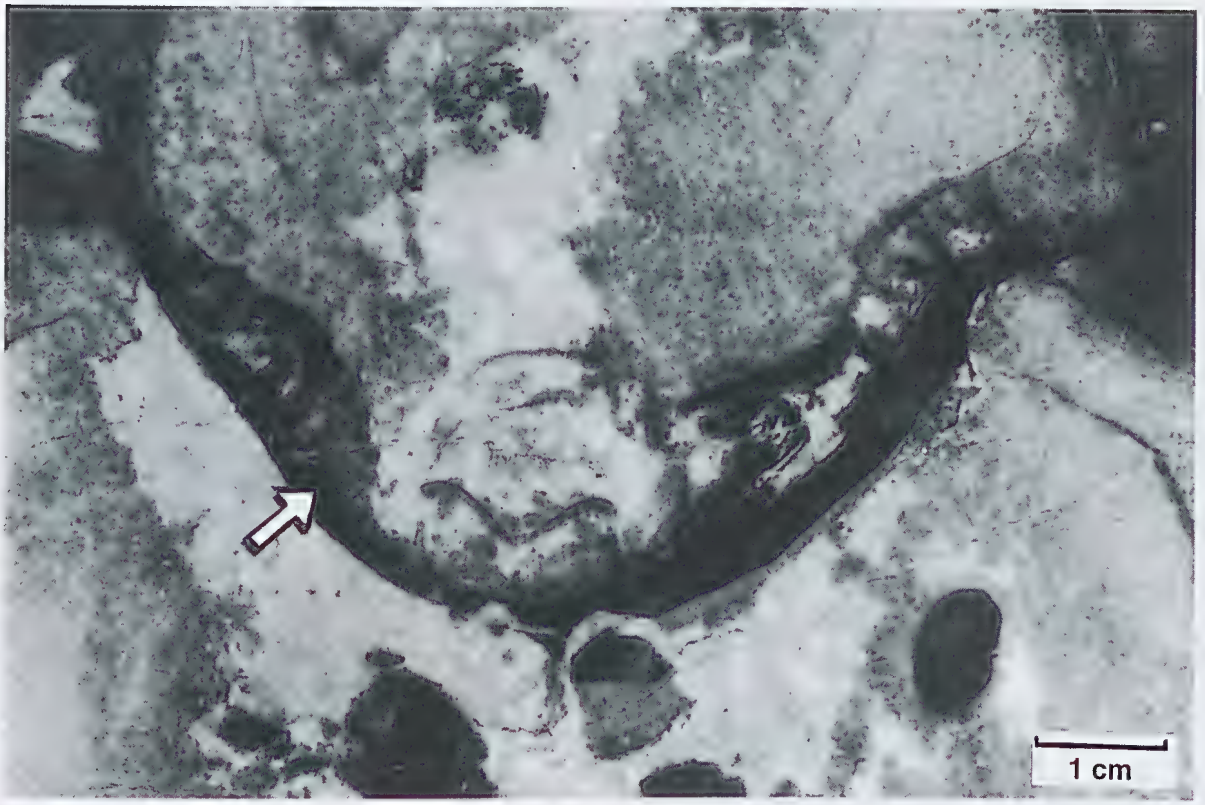

Figure 8. A peel taken from a transverse serial section of paratype MMF 33364, at 60.3 mm from the posterior end; 1 cm scale bar. The swollen articulating plate (arrowed), and the slots it conceals (which we interpret as locations of diductor attachment), are clearly visible in the centre of the photograph, as is the trace of the dorsal platform. At right can be seen the relationship between the valve margins at the pivot zone. Note the heavy but irregular recrystallisation.

directly on to the valve floor—platforms were not developed. The shell was thick and solid, without umbonal excavation to lighten the valves. *Ussunia* has no form of mechanical articulation, and the dorsal beak showed no sign of enrolling. *Keteiodoros* averages 4 to 5 times the length and width of *Ussunia*, and is about 7 times as globose. The two genera are separated in time by about 35 million years; *Ussunia* represents the small unspecialised ancestral stock, while *Keteiodoros* is the highly specialised, complex and gigantic descendant on a line soon to pass into oblivion. Cope's Rule was rarely more clearly expressed.

Functional morphology. The most distinctive feature of this new trimerellide, apart from its size and strong biconvexity, is the inferred method of articulating the valves. This involves the valve margins, the dorsal umbo, and the pseudointerarea.

Polished and serial sections (e.g., Figs. 6, 11), and prepared shells (Fig. 7), show that the dense posterior part of the dorsal valve, greatly enlarged and extremely strongly incurved, fitted laterally within the limits of the posteriorly equally dense ventral platform and pseudointerarea. In front of this region where the dorsal umbo sat within the pseudointerarea over its full width, the lateral margins of the dorsal valve expanded rapidly, such that a solid shelf formed on each side which rested on the flattened top of the ventral valve margin (Fig. 6, from 55.7 mm; Fig. 8). This zone of flattened valve margins was short, and was where the margins crossed over one another as seen dorsoventrally. These flattened zones are inferred to have acted as pivots (not teeth and sockets) for the opening and closing of the shell. This is a form of articulation which, while rudimentary, is nevertheless somewhat reminiscent of that in some non-strophic rhynchonellate shells such as pentamerides. In front of the pivot zone each dorsal valve margin developed a broad somewhat oblique groove, into which fitted a similarly oblique flange arising from the inner edge of the ventral valve margin (Figs. 6, 7, 12). Functionally, the result was an interlocking system which, when the shell was closed, prevented relative movement of the two valves in the plane of commissure. When the shell was open, the close fit of the dorsal umbo in the pseudointerarea probably also constrained by the position of the adjacent muscles, would have provided significant restraint on relative lateral and skewing movements between the valves.

None of the available material is well enough preserved to show muscle scars but, if one considers the musculature involved in shell articulation, it can be assumed that the adductors would have extended from one platform to the other, as inferred for other trimerellides (Norford & Steele, 1969, text-fig. 2; Mergl, 1989). Given the size and probable weight of the valves, the considerable strength of such short thick muscles would probably have been very necessary to close the shell, and even more so to keep it

Figure 9. Paratype MMF 33365, a silicified fragment of a dorsal umbo, in approximately ventral (top) and lateral (bottom) aspects; 1 cm scale bar. Note the distinct asymmetry of the sharp incurved beak (apical angle 110°, directed right-ventrally at about 60° to the commissure), and the tracks of the bottom edges of the dorsal platform. Only the proximal part of the articulating plate is preserved, but its relationship to the beak is clear. The flat-bottomed ridged channel between beak and plate (compare Figs. 8, 10) we interpret as the site of diductor attachment.

closed against adverse conditions. However, the method of opening the shell poses problems, especially in view of the close fit between pseudointerarea and dorsal umbo.

Muscles extending forward from the anterior surface of the dorsal umbo to the ventral platform upon contraction would have served not to open the shell, but simply to pull the dorsal valve forward (which the interlocking of the valve margins and the bulge on the ventral platform in front of the dorsal umbo would have prevented anyway). To achieve proper leverage, muscles operating as diductors (we have no way of establishing precise homologies, so in this paper use the term "diductors" in a purely functional sense, as the muscles responsible for opening the shell) must have extended forward from somewhere on the dorsal umbo behind or ventral to the above-described marginal pivot zones. Muscles attached to the distal face of the curved articulating plate and extending to an attachment area well forward on the ventral platform would have met this criterion, but there are two difficulties: when the shell was closed, there would have been little if any room between plate and platform for passage of the muscles, and contraction of the muscles would have put significant strain on the base of the plate, possibly enough to break it. Examination of serial and longitudinal sections, and of the silicified specimens, suggests an alternative (Fig. 13): that the dorsal ends of the diductors were attached to the umbonal surface in the lateral slots at the sides of the articulating plate, and emerged to either side of the plate. There are appropriate gaps at the sides of the dorsal umbo between sections at 55.7 and 60.8 mm in Fig. 6, approximately aligned with, but ventral to, the marginal pivot zones, and also in the peels from MMF 33364, Fig. 8. As already noted, MMF 33365 and 33366 reveal appropriately situated striated areas suitable for such attachment. With the diductors attached to the outer parts of the ventral platform in front of its mid-length, there would have been adequate space for the viscera and adductors medially. Mechanically this would have formed an effective lever system, opening the shell about the proposed pivot points to at least a 10° gape and possibly as much as 20°. However, one effect of such a system is that the dorsal umbo would have slid on the pseudointerarea unless restrained by soft tissue and periostracum. The geometry visible in longitudinal sections would have allowed for this movement, and the posterior geometry of the shell appears to be such that neither the exterior space between the two umbos (which is in any case not very large) nor the visceral space posterior to the dorsal umbo changed significantly during such a movement. The laminated pad on the floor of the pseudointerarea occupying the zone where such sliding would have occurred, may have formed a bearing surface for such movement, perhaps also serving by a close fit of the two surfaces to exclude sediment. Moreover, the articulating plate would have protected the dorsal ends of the laterally placed muscles from damage during such movement. A thickened zone of periostracum may have been present, but this is uncertain because of the state of preservation of the shells.

The manner of posterior closure, and the way in which the valves moved during opening, is important, because the shells sat freely umbo-down in sediment, and the space between dorsal and ventral umbos could only have been occupied by either tissue or silt. There appears to be no room for passage of a pedicle (in common with other trimerellides), and so it is unlikely there was organic tissue filling the space, but unless the silt were either extremely soft and fluid (thixotropic?) or shaped by the animal into a firm stable cavity, it would have been an impediment to valve opening. The proposed opening mechanism would not have been strong enough to work against loose but resistant material, and the diductors would probably have served (in conjunction with relaxation of the adductors) simply to initiate opening. This is supported by the observation that the weight distribution of the dorsal valve about the pivots appears to have been evenly balanced when the shell was closed. The large solid beak on the ventral side of the pivot-line was balanced by the larger volume of thinner-walled platform

Figure 10. Paratype MMF 33366, a well-preserved silicified fragment of a dorsal valve interior, in anteroventral aspect at left (1 cm scale bar), and with the umbonal region enlarged in oblique lateral view at right. The dorsal beak is not preserved. The posterior part of the dorsal platform is gently concave longitudinally and strongly vaulted anteriorly, producing a shallow median longitudinal depression which gradually widens anteriorly. Supporting the platform above the now-missing valve floor is a Y-shaped septum. At the broken anterior end of the platform, a small triangular cavity is formed between the divergent arms of the Y and the overlying platform floor. Anteriorly the platform is approximately 30 mm wide, and is estimated to have stood above the valve floor by at least 23 mm. At the posterior end of the platform, a thin median septum (?= cardinal buttress) about 10 mm long extends nearly vertically from the platform floor, expanding posterodorsally to merge with a bulbous medial expansion at the base of the articulating plate. The greater part of the articulating plate is broken away, revealing a horizontally ovoid cross-section. As in MMF 33365 there is asymmetry present: in the aspect figured at left, the septum and articulating plate bulge display a slight but obvious anticlockwise rotation. The articulating plate is much more robust than that in MMF 33365, which was possibly from a juvenile individual. The lateral edges of the articulating plate are flattened and slightly extended, giving the base of the plate a broadly lanceolate cross-section. There are growth lamellae on the posterior surface of the plate, which is separated from the remnant of the valve margin by a deep channel (compare Fig. 9).

and shell wall making up the anterior part of the valve. Stability in that position was increased by the solid shell mass making up that part of the dorsal valve posterior to (hence below) the pivot-line. However, once opening movement was initiated, the weight of the anterior part of the dorsal valve, moving through a perceptible arc, would have overcome the weight of the dorsal umbo which barely changed its orientation relative to the pivot zone.

The considerable weight of the dorsal valve would have required the constraint of strong adductor muscles to stop it from sliding downwards out of the bearing surface formed by the pseudointerarea. The size and elevation of the platforms suggests that the adductors were indeed strong, but this function may also have been aided by the close conjunction of the distal end of the articulating plate with the terraced face of the tissue pad which formed the bearing surface on the top of the pseudointerarea. Moreover, at least in gerontic shells the strongly incurved ventral beak formed a cup effectively restraining the dorsal valve from below. A further implication of the weight of the valve is that closing the shell would at least initially have required the strong adductors suggested above.

Phylogenetic relationships

The new genus is characterised by gigantic size and a unique articulatory mechanism comprising dorsal articulating plate, robust zones on the edges of the ventral valve pivoting against equally robust zones on the dorsal margins, and, in front of those zones on the valve margins, oblique ventral flanges restraining twisting movement by articulating with marginal dorsal "sockets" (Fig. 12). These and other associated morphological features adapted *Keteiodoros* well to its preferred environment.

Taken by themselves, tendencies towards gigantism or oblate/spheroidal shape have relatively little phylogenetic significance. For example, *Adensu* Popov & Rukavishnikova, 1986, is a monotypic Late Ordovician trimerellide, endemic to Kazakhstan, which has a similar shape to, and dimensions approaching those of *Keteiodoros*. However, *Adensu* lacks both raised muscle platforms and umbonal cavities, and its articulating plate lies parallel to the commissure. Accordingly it is not thought to be closely related to *Keteiodoros*.

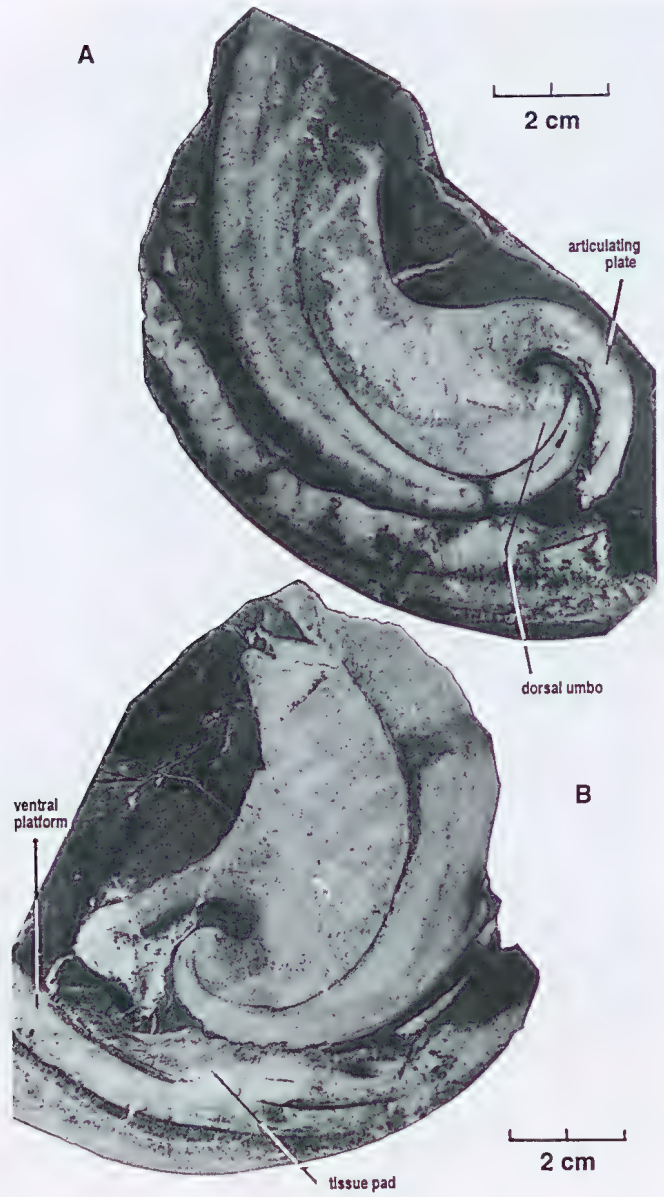

Figure 11. **A–B**—axial longitudinal sections of two incomplete shells. **A**—AM F101121; **B**—AM F101120 (2 cm scale bars) showing the present relationship between the dorsal umbo and ventral platform, the curved articulating plate which is inferred to cover the dorsal ends of the diductor muscles, and the layered pad of tissue on the pseudointerarea against which the dorsal umbo may have moved during opening and closing (compare Figs. 7, 12). Note also the strong spiral trace of the surface of the dorsal platform, and the extensive recrystallisation.

Substantial umbonal shell thickening is a typical means in many unrelated brachiopods (e.g., pentamerides) of preventing dislodgement by waves or currents of shells lacking pedicle or cementation attachment. Long umbonal cavities are likewise common to most known Silurian trimerellide genera, as are prominent ventral platform vaults. The only known trimerellides with strongly vaulted dorsal platforms are *Paradinobolus* Li & Han, 1980 and *Prosoponella* Li, 1984 (both from the early Ashgill of South China), and the widely distributed and long-ranging *Trimerella* (late Ordovician to middle Silurian). A single silicified incomplete dorsal valve with such a platform,

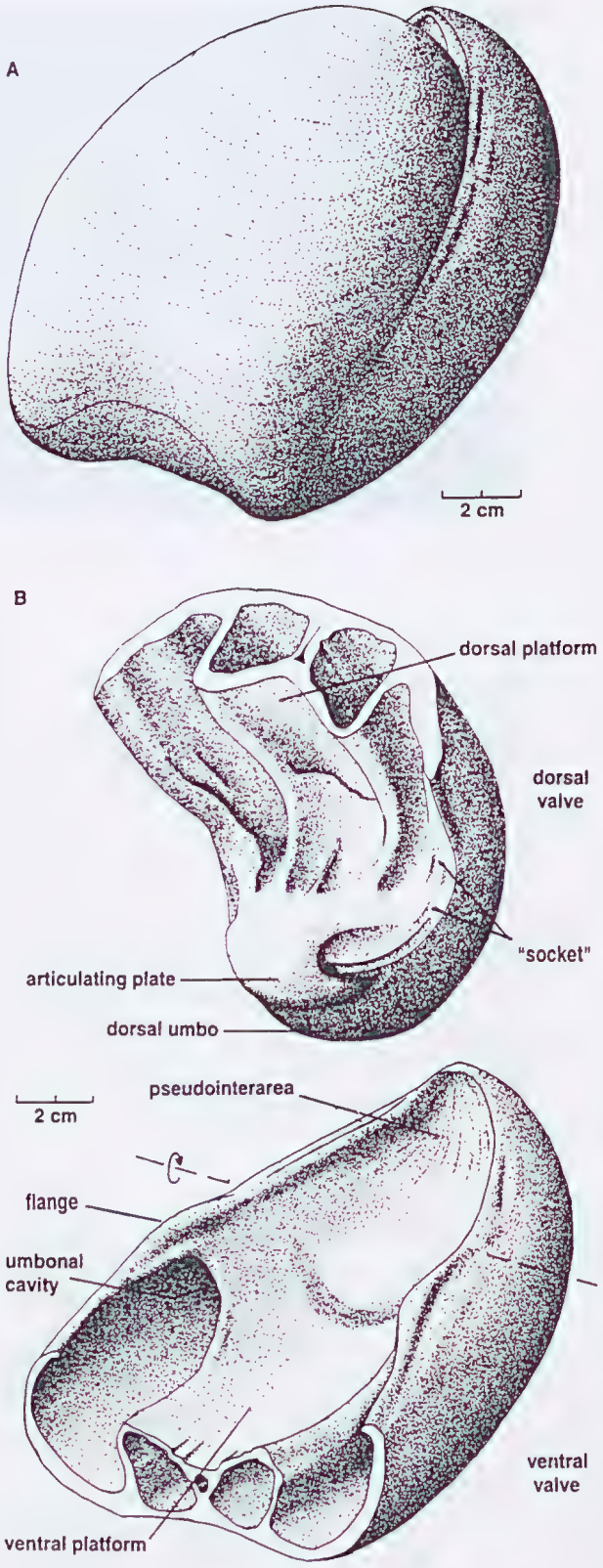

Figure 12. **A–B**, oblique views of the shell exterior (**A**) and interior (**B**) of *Keteiodoros bellense* n.sp., reconstructed from the complete paratype AM F101117 (Fig. 4) and serially sectioned paratype CPC 34409 (Fig. 6), and modified after the holotype (Fig. 7) and the silicified dorsal valve, paratype MMF 33366 (Fig. 10); 2 cm scale bars. In B, the open valves have been truncated anteriorly to show their cross-sections, while the dorsal valve has been strongly rotated, and lifted vertically above the ventral valve, to show its interior; the inferred position of the "hinge" line is shown as a dashed line.

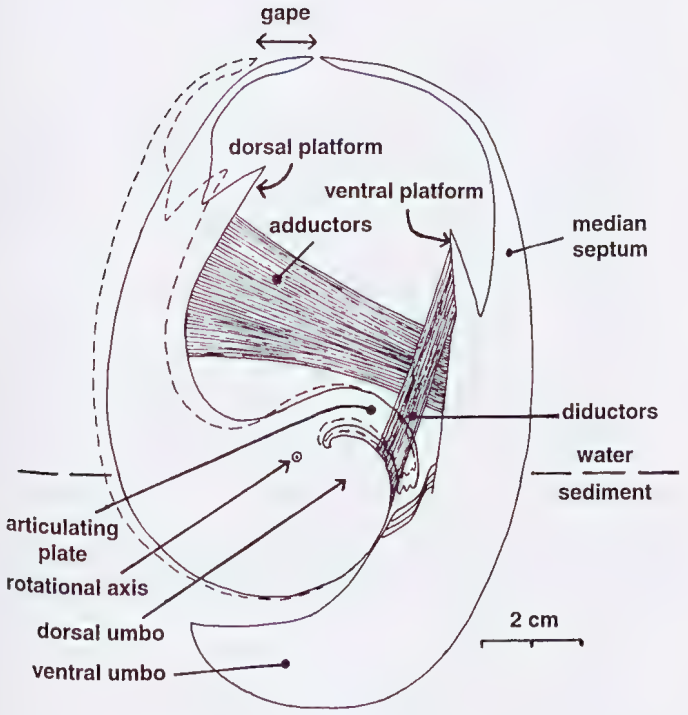

Figure 13. Reconstructed axial longitudinal section of a shell, with the inferred positions of the adductor and diductor muscles projected onto that plane. A dashed line gives the dorsal valve in open position, showing the minimum amount of gape possible under this scheme. Based on the serially sectioned shell, which has been used to project the axis of rotation of the dorsal valve from its inferred position at the valve margins, and on the longitudinal section of AM F101121 (Fig. 11A).

referred doubtfully to *Paradinobolus*, is also known from the Late Ordovician Malongulli Formation in central New South Wales. Superficial similarities aside, none of these trimerellides share sufficient characters in common with *Keteiodoros* to be considered directly related.

The specialised articulatory mechanism of *Keteiodoros* is likely to provide the best clue to its evolutionary relationships. One trimerellide, *Belubula spectacula* Percival, 1995, from the Late Ordovician (early Eastonian, equivalent to late Caradoc) Belubula Limestone of central New South Wales, is a potential ancestor to *Keteiodoros*. Although separated in time by approximately 25 million years, and without intervening evolutionary stages being known at present, the two genera share significant morphological similarities, habitat preferences, and geographic proximity. *Belubula* is of gigantic size for Late Ordovician trimerellides, reaching an estimated 200 mm in length and 100 mm in width; the largest individuals are thus comparable in length with *Keteiodoros*, though the latter is relatively much wider and deeper. In profile, both are similarly strongly equibiconvex. Note also that both genera display asymmetry (compare Percival, 1995: Fig. 4J with MMF 33365, Fig. 9), although the direction of asymmetry of only the ventral valve of *Belubula* is apparent from the figure. Grossly thickened posterior regions of the ventral valves in both *Keteiodoros* and *Belubula* contain large conical umbonal cavities. Of particular significance is one gerontic individual of *Belubula* (Percival, 1995: Fig. 4C) which exhibits an incipient modification of the dorsal homeochilidial (or articulating?) plate which could well have led to the specialised articulation of *Keteiodoros*. Percival (p. 50) noted in reference to this particular silicified dorsal valve that in gerontic specimens this plate "can enlarge to form a prominent curved bulbous plate, bearing growth striations, & extending ventrally above level of commissure with a knife-edge anteroventrally". It is reasonable to suggest that over the ensuing 25 million years of evolution this plate developed into the robust incurved articulating plate of *Keteiodoros*, bearing a median bulge and buttressed anteriorly by a median ridge, and forming part of a large ball-like dorsal umbo bearing against the concave pseudointerarea. Whereas a massive muscle (attached to the ventral cardinal socket and inserted in the dorsal subcardinal depression) was essential in *Belubula* to prevent a shearing motion of the valves during articulation, paired diductors attached at the sides of the articulating plate, lateral to the ball joint, could have served the same purpose in *Keteiodoros*.

ACKNOWLEDGMENTS. In reconciling the initially divergent ideas on aspects of this unusual brachiopod, a large part has been played by the technical help we have received, and for which we are grateful. Michael Doyle of AGSO had the difficult task of mechanically preparing specimens, made the first set of serial sections, and did much of the photography. At the University of Wollongong Andrew Southall prepared peels from the serial sections, and Trudi Marshall prepared drawings from those peels. Gary Dargan of the Geological Survey of N.S.W. prepared further sections and the silicified specimens, while David Barnes photographed them. We would also like to thank Lars Holmer and reviewers Michael Bassett and Jisuo Jin for their interesting and useful comments. John Pickett and Ian Percival publish with permission of the Director-General, New South Wales Department of Mineral Resources. Desmond Strusz completed the paper while a Visiting Fellow in the Geology Department, Australian National University, and would like to thank Prof. Arculus for providing the necessary facilities.

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The Amphipoda (Crustacea) of New Caledonia: Aoridae

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ABSTRACT. Fourteen species of Aoridae are recorded from New Caledonia. Seven species are described and figured in full, including one genus and five species new to science and two species presented in new nomenclatural combination. A further three species are partially figured. New Caledonia is shown to display Australian plate biogeographic relationships.

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Collections of marine amphipods were made by the writer, J.K. Lowry and I. Takeuchi in Grande Terre, New Caledonia, and in the Loyalty Islands during October and November, 1995. Fourteen species of Aoridae in seven genera were collected and are reported on here. Of these, one genus and four species are new to science. Six species are currently thought to be New Caledonian endemics.

Of the fourteen Aoridae reported from New Caledonia, seven are, as far as is currently known, endemic. This is more endemic aorids than has Fiji, 43% (Myers, 1985b), Madang Lagoon 30% (Myers, 1995), Samoa, 20% (Myers, 1997) or Tonga (Myers, 1986), which has no endemic aorids. New Caledonia and Fiji in addition to their high species endemicity, also each have an endemic aorid genus.

Seven New Caledonian species have extrinsic distributions, three, *Bemlos aequimanus, Bemlos waipio* and *Globosolembos excavatus* have wide Indo-Pacific distributions. Three species, *Bemlos tui, Bemlos saloteae* and *Globosolembos lunatus* occur within the area bounded by Samoa and Tonga in the east and Papua New Guinea and eastern Australia in the west. *Xenocheira* sp. is reported from Australia but may be synonymous with *X. seurati* recorded from Fiji and the Gambier archipelago.

With regard to the Aoridae, New Caledonia therefore shows rather typical Australian plate relationships, sharing taxa to the west with Australia and Papua New Guinea and to the north and east with islands on the Vanuatu-Tonga island arc.

The following abbreviations are used in the figures: A, antenna; Lb, labrum; Mx, maxilla; Md, mandible; Mxp, maxilliped; L, labium; G, gnathopod; P, pereopod; Ep, epimeron; U, uropod; T, telson. AM, Australian Museum, Sydney; NCL, New Caledonia; ORSTOM, Organisation de Recherche Scientifique Territoire Outre-Mer. All material is ultimately to be deposited in the Australian Museum. The type material is in the Australian Museum.

Systematics

Family Aoridae

Aora Krøyer

Aora aoriformis (Ledoyer) n.comb.

Figs. 1–2

Lembos aoriformis Ledoyer, 1984: 33, fig. 15.

Material examined. NCL-28 (3 ♂♂, 3 ♀♀), NCL-31 (1 ♀), NCL-95 (3 ♂♂, 6 ♀♀), NCL-97 (1 ♂), NCL-98 (10 ♂♂, 17 ♀♀), NCL-111 (4 ♂♂, 5 ♀♀), NCL-112 (2 ♀♀), NCL-113 (2 ♂♂, 3 ♀♀), NCL-116 (1 ♂, 8 ♀♀, 2 immature), NCL-128 (1 ♂, 2 ♀♀), NCL-129 (25 ♂♂, 34 ♀♀), NCL-130 (2 ♂♂, 13 ♀♀).

Description. Male and female to 3.5 mm. Male pereon segments lacking sternal processes. Head lateral lobes only moderately produced; eye relatively large, situated proximal to lobes; distoventral margin poorly recessed, shallow. Antenna 1 markedly longer than body; peduncular articles in the basi-distal length ratios 7:12:3; accessory flagellum well developed with 4 articles, the terminal article rudimentary, flagellum poorly setiferous, over twice length of peduncle, with about 33 articles, all except the most proximal with aesthetascs. Antenna 2 only moderately setiferous, less than half length of antenna 1; peduncular articles 4 and 5 subequal in length; flagellum subequal in length with peduncular article 5 with 7 articles, the terminal ones with strong setae. Mouthparts conforming to normal *Aora* structure; mandible palp article 3 subequal in length with article 2, slender, posterior margin convex with a few long marginal setae and an understory of short setae. Male gnathopod 1 weakly setiferous; coxa strongly produced forward, subacute; basis elongate, anterior margin with strong acute or subacute medial spine; merus produced into acute ending tooth, shorter than and weakly deflected from the carpus; carpus subrectangular, parallel-sided; propodus subrectangular, subequal in width with carpus, palm obsolete; dactylus large, falcate, only a little shorter than propodus. Female gnathopod 1 coxa subrectangular deeper than broad; merus unproduced; carpus subtriangular, shorter than that of male; propodus and carpus subequal in length, palm very oblique defined by a stout seta; dactylus of moderate length, slightly overlapping palm. Male gnathopod 2 coxa subround; basis slender, anterior margin concave; carpus and propodus subequal in length, only moderately setiferous; propodus subrectangular, palm oblique, defined by a spine; dactylus fitting palm. Female gnathopod 2 coxa much larger than that of male; basis a little more slender than that of male, with anterior margin substraight; carpus a little shorter than propodus, subtriangular; propodus palm evenly convex, defined by a stout seta; dactylus short, fitting palm. Pereopods 5–7 in the length ratios 4:7:9; propodus posterior margin with stout setae distally. Epimera 2–3 each with a small distoventral tooth. Uropod 1 peduncle a little longer than outer ramus and with strong distoventral spine about one third length of peduncle; outer ramus a little longer than inner; both rami with marginal stout setae. Uropod 2 peduncle shorter than inner ramus and with short triangular distoventral spine; inner ramus distinctly longer than outer; both rami with marginal stout setae. Uropod 3 rami longer than peduncle; rami subequal in length; outer ramus with slender distal setae, one marginal seta and with small second article; inner ramus with marginal stout seta and a slender distal seta. Telson dorsolateral crests each with three slender setae.

Remarks. This species is small and fragile. The large, pale eye allows separation of freshly preserved (in alcohol) specimens of this species from *A. spinimerus*, which is sometimes found in the same samples.

This species was originally assigned to the genus *Lembos* by Ledoyer (1984) based on the male gnathopod merus being shorter than the carpus, male coxa 1 being of the "*Lembos*" type, presumably referring to the forward produced, anterodistal margin and the mandibular palp being weakly falcate with a row of small setae. The shortened male gnathopod 1 merus is unusual in *Aora*, but occurs also in *A. spinicornis*, the acute coxa occurs in several *Aora* species e.g., *A. typica, A. hebes* and *A. spinicornis* and the mandible palp is similar to that of *A. hircosa*. In all respects this and the following species conform to the genus *Aora* Krøyer.

Habitat. Amongst *Padina, Sargassum*, seagrasses and coral rubble , 0–10 m.

Distribution. New Caledonian endemic.

Aora spinimerus (Ledoyer) n.comb.

Figs. 3–4

Lembos spinimerus Ledoyer, 1984: 37, fig. 17A.

Material examined. NCL-4 (1 ♂), NCL-15 (1 ♂), NCL-21 (6 ♂♂, 9 ♀♀), NCL-25 (4 ♂♂, 9 ♀♀, 1 immature), NCL-26 (3 ♀♀, 2 immature), NCL-28 (9 ♂♂, 16 ♀♀, 1 immature), NCL-29 (1 ♂, 2 ♀♀, 2 immature), NCL-33 (2 ♀♀), NCL-40 (2 ♀♀, 1 immature), NCL-47 (5 ♂♂, 6 ♀♀, 2 immature), NCL-49 (3 ♂♂, 1 ♀, 1 immature), NCL-60 (1 ♂, 3 ♀♀), NCL-63 (1 ♂), NCL-64 (1 ♂, 2 ♀♀), NCL-68 (2 ♀♀), NCL-79 (1 ♂, 2 ♀♀), NCL-98 (2 ♂♂, 4 ♀♀), NCL-110 (2 ♂♂), NCL-111 (3 ♂♂, 5 ♀♀), NCL-112 (1 ♀), NCL-116 (4 ♂♂, 11 ♀♀, 1 immature), NCL-128 (1 ♀), NCL-129 (6 ♂♂, 9 ♀♀), NCL-130 (4 ♂♂, 6 ♀♀), NCL-139 (12 ♂♂, 9 ♀♀, 3 immature), NCL-153 (3 ♂♂, 1 ♀), NCL-154 (1♂, 2 ♀♀, 1 immature), NCL-156 (1 ♂, 3 ♀♀), NCL-237 (7 ♀♀), NCL-246 (1 ♂, 3 ♀♀).

Description. Male and female to 5.5 mm. Male pereon segments lacking sternal processes. Head lateral lobes only moderately produced; eye moderately large situated proximal to lobes; distoventral margin poorly recessed, shallow. Antenna 1 a little shorter than body length; peduncular articles in the basi-distal length ratios 3:4:1;

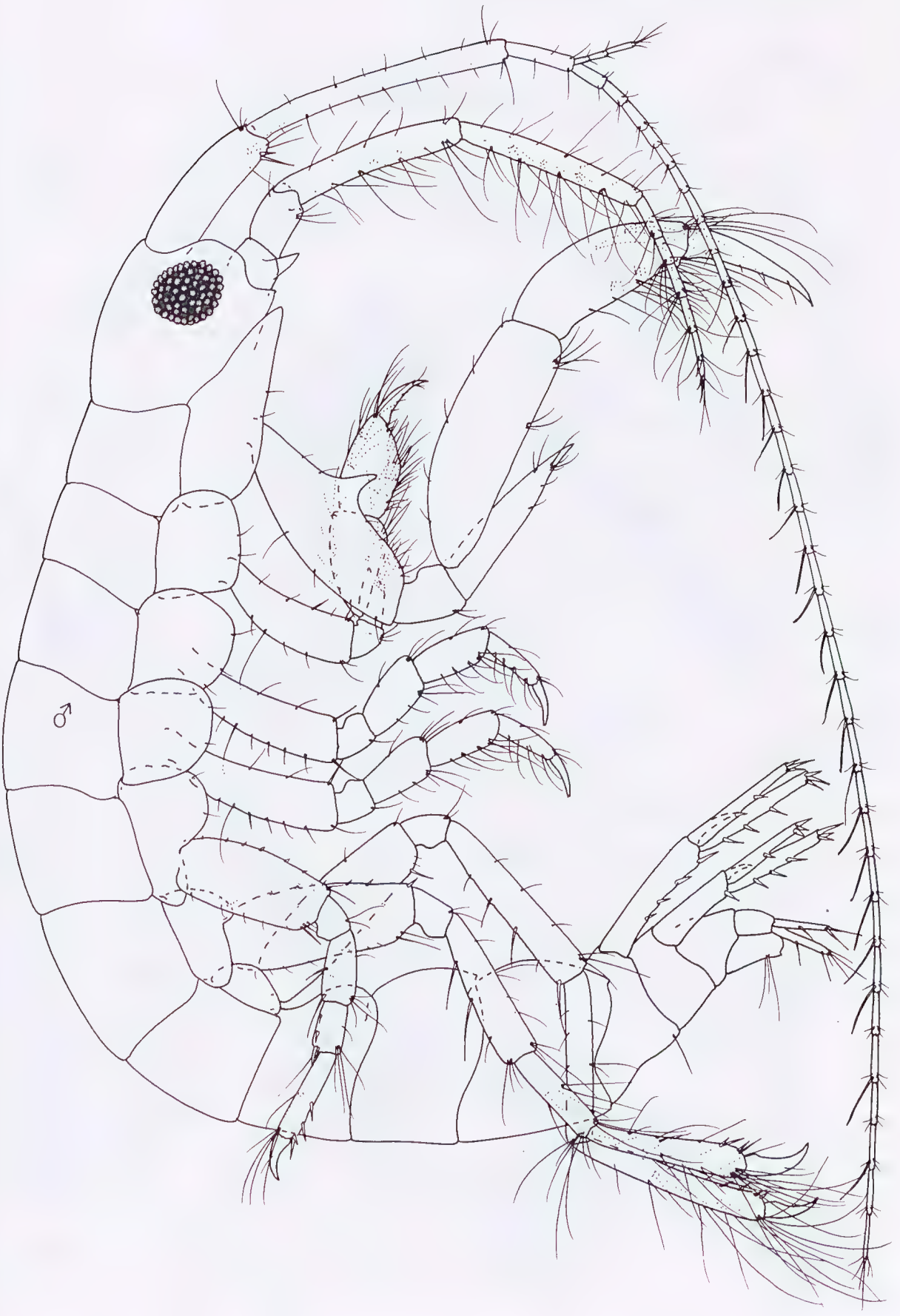

Figure 1. *Aora aoriformis* (Ledoyer). Off Ilot Maitre, Noumea Lagoon, New Caledonia, NCL-98.

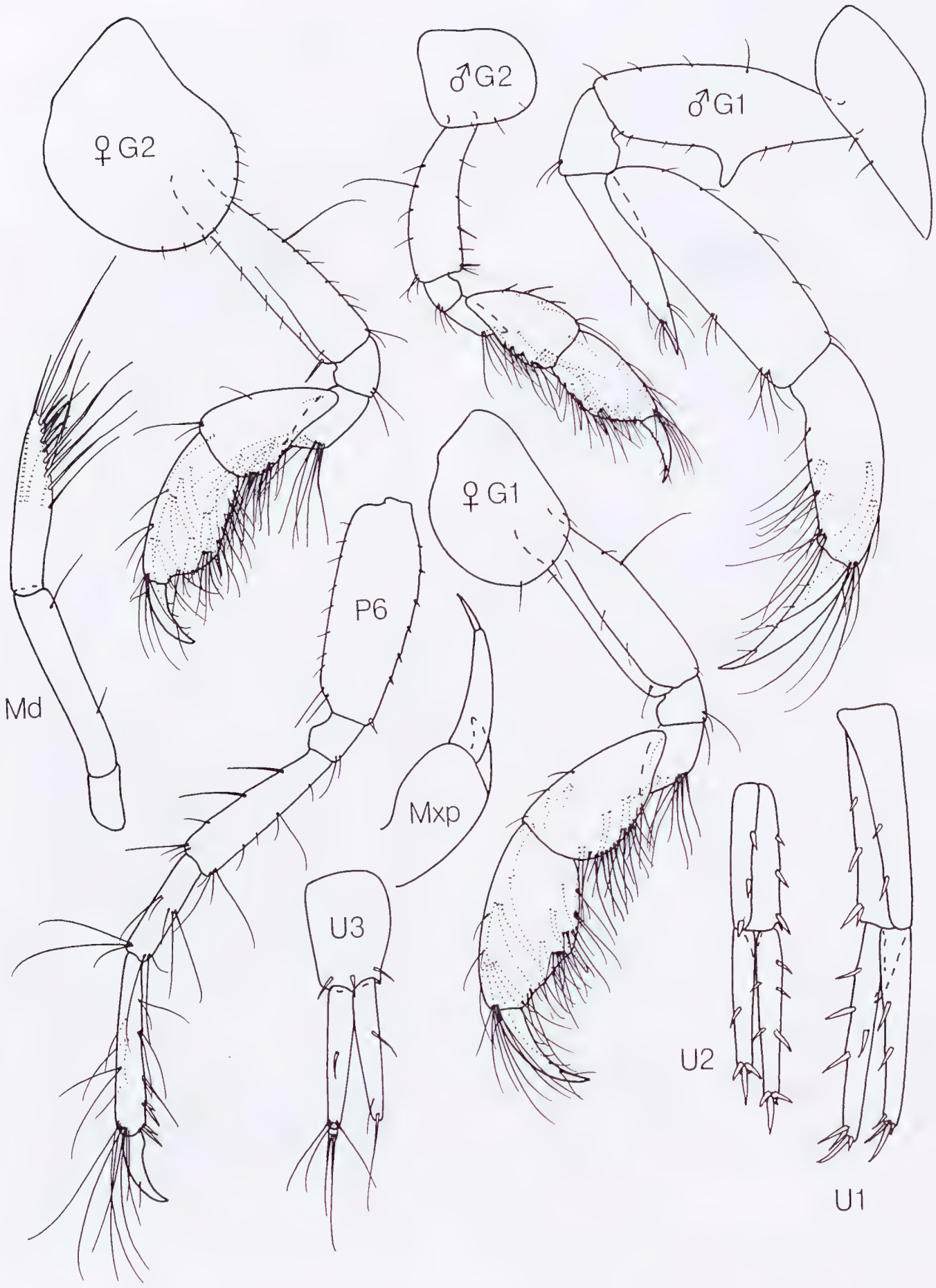

Figure 2. *Aora aoriformis* (Ledoyer). Off Ilot Maitre, Noumea Lagoon, New Caledonia, NCL-98.

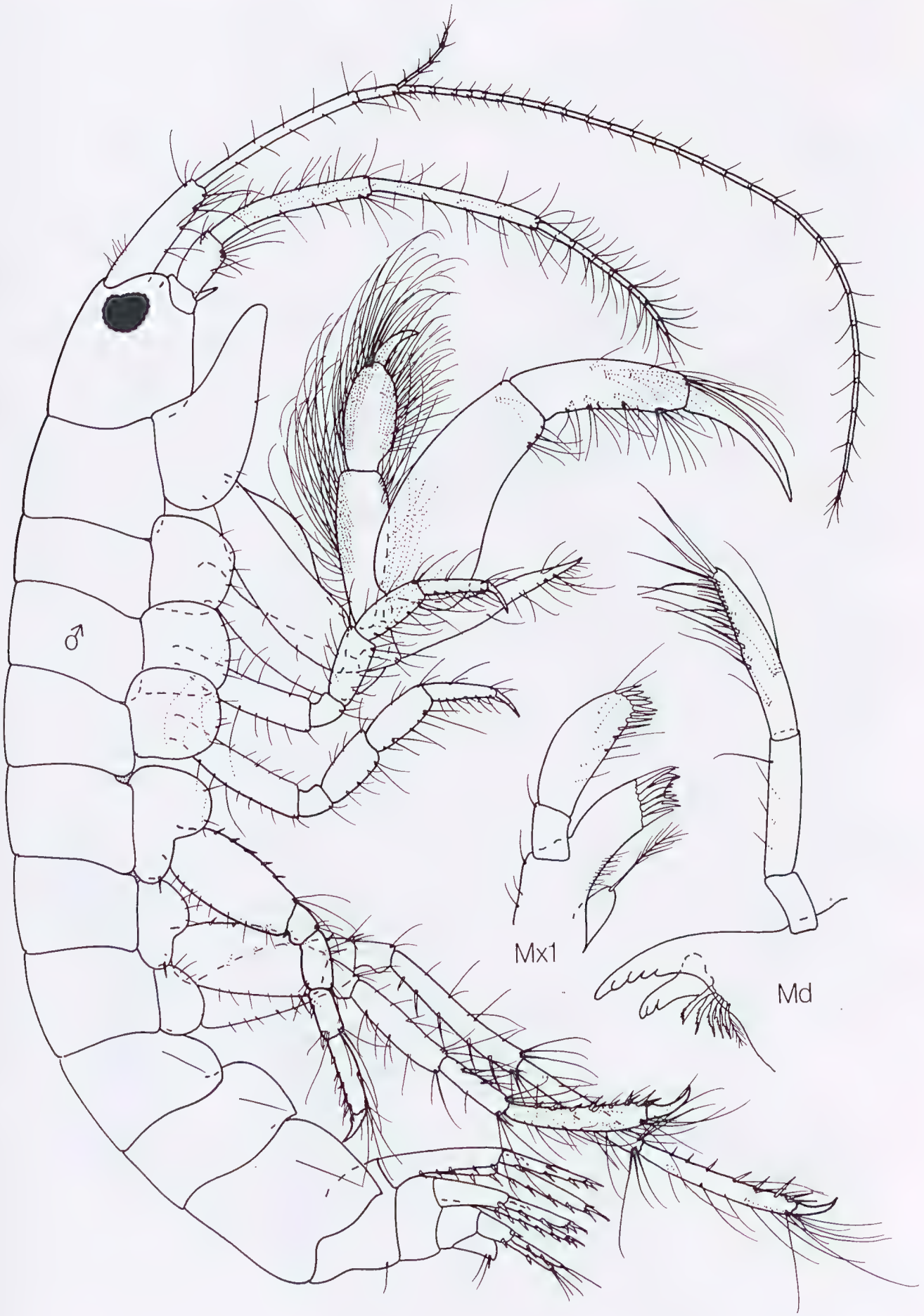

Figure 3. *Aora spinimerus* (Ledoyer). Between Ilot Maitre and Croissant reef, Noumea Lagoon, New Caledonia, NCL-28.

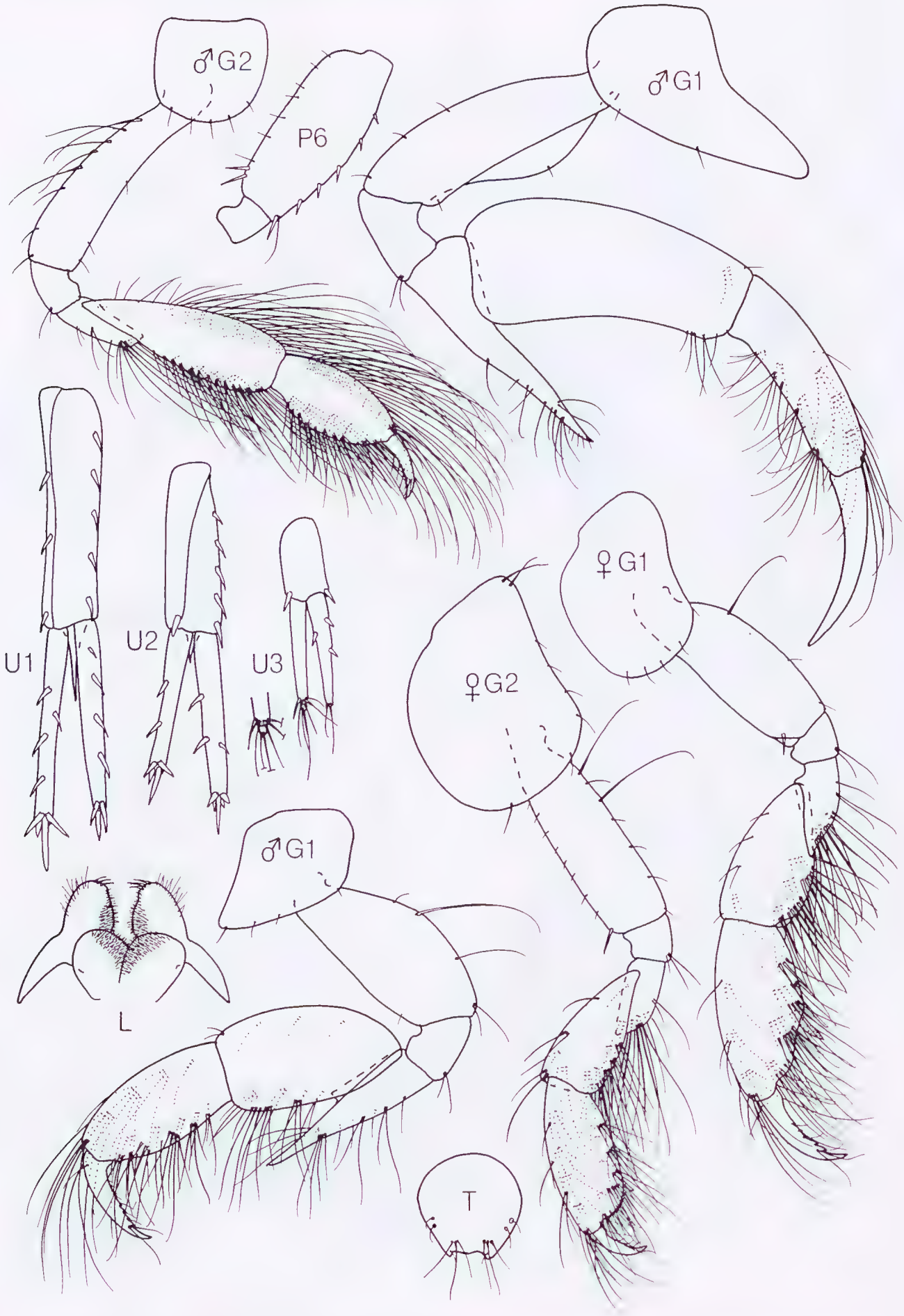

Figure 4. *Aora spinimerus* (Ledoyer). Between Ilot Maitre and Croissant reef, Noumea Lagoon, New Caledonia, NCL-28.

accessory flagellum well developed with six articles, the terminal article rudimentary; flagellum poorly setiferous, twice length of peduncle, with about 30 articles. Antenna 2 only moderately setiferous; two-thirds length of antenna 1; peduncular articles 4 and 5 subequal in length; flagellum subequal in length with peduncular article 5 with 7 articles, the terminal ones with strong setae. Mouthparts conforming to normal *Aora* structure, mandible palp article 3 longer than 2, slender, posterior margin substraight with a few long marginal setae and an understory of short setae. Male gnathopod 1 weakly setiferous; coxa strongly produced forward, subacute; basis elongate, anterior margin with rounded flange; merus produced into acute ending tooth, shorter than and strongly deflected from the carpus; carpus subrectangular, broader proximally; propodus subrectangular but more slender than carpus, palm obsolete; dactylus large, falcate, only a little shorter than propodus. Female gnathopod 1 coxa subrectangular deeper than broad; merus unproduced; carpus subtriangular, shorter than that of male; propodus a little longer than carpus, palm very oblique defined by a stout seta; dactylus of moderate length, fitting palm. Male gnathopod 2 coxa subround; basis elongate and slender; carpus elongate over three times as long as broad, anterior margin with dense brush of long setae; propodus subovoid, about two thirds length of carpus, anterior margin with dense brush of long setae, palm oblique, scarcely distinct from posterior margin; dactylus short. Female gnathopod 2 coxa much larger and basis less slender, than that of male; carpus a little shorter than propodus, subtriangular; propodus palm evenly convex, defined by a stout seta; dactylus short, fitting palm. Pereopods 5–7 in the length ratios 6:9:12; propodus posterior margin with stout setae. Epimera 2–3 each with a small distoventral tooth. Uropod 1 peduncle a little longer than outer ramus and with strong distoventral spine a little less than one third length of peduncle; outer ramus a little longer than inner; both rami with marginal stout setae. Uropod 2 peduncle subequal in length with inner ramus and with short triangular distoventral spine; inner ramus distinctly longer than outer; both rami with marginal stout setae. Uropod 3 rami longer than peduncle; rami subequal in length; outer ramus with slender distal setae, but lacking marginal setae and with small second article; inner ramus with marginal stout setae and a pair of slender distal setae. Telson dorsolateral crests each with three slender setae.

Remarks. Adult material of this species was not available to Ledoyer (1984). It is therefore figured here and redescribed in more detail. This species is larger and more robust than the preceding species. For other separating characters see remarks on that species.

Habitat. Amongst *Padina, Sargassum*, large yellow sea fans, rubble and red algae and fine sand, 0–38 m.

Distribution. New Caledonian endemic.

Bemlos Shoemaker

Bemlos aequimanus (Schellenberg)

Lembos aequimanus Schellenberg, 1938: 76, fig. 39.–Barnard, 1965: 527, fig. 26.–Barnard, 1970: 72, figs. 36a–c.–Ledoyer, 1984: 31, fig. 14.–Myers, 1985c: 385, figs. 246–248.
Bemlos aequimanus.–Myers, 1988a: 188.–Myers, 1995: 30.

Material examined. NCL-2 (3 ♂♂, 5 ♀♀, 1 immature), NCL-7 (1 ♀, 1 immature), NCL-8 (2 ♂♂, 2 ♀♀), NCL-9 (1 ♂), NCL-10 (2 ♀♀), NCL-11 (1 ♂), NCL-12 (1 ♀), NCL-15 (10 ♂♂, 13 ♀♀, 2 immature), NCL-17 (8 ♂♂, 7 ♀♀), NCL-18 (6 ♂♂, 6 ♀♀, 2 immature), NCL-19 (11 ♂♂, 12 ♀♀, 3 immature), NCL-21 (3 ♂♂, 1 ♀, 1 immature), NCL-22 (4 ♂♂, 4 ♀♀, 3 immature), NCL-80 (2 ♂♂, 1 ♀, 2 immature), NCL-212 (1 ♀, 1 immature).

Remarks. New Caledonian material does not appear to differ significantly from that reported from other Pacific islands.

Habitat. Amongst sea grasses, red and brown algae, spherical rhodoliths and coral rubble, 0–2 m.

Distribution. Hawaii, Marshall Islands, Kiribati, Tonga, Western Samoa, Papua New Guinea, New Caledonia.

Bemlos waipio (Barnard)

Lembos processifer Barnard, 1965: 529, figs. 28g–m (not *Lembos processifer* Pirlot, 1938).
Lembos waipio Barnard, 1970: 85, figs. 44–45.–Myers, 1985c: 379, figs. 242–245.
?*Lembos waipio*.–Ledoyer, 1984: 37, fig. 17B.
Bemlos waipio.–Myers, 1988a: 189.–Myers, 1995: 30.

Material examined. NCL-2 (1 ♂), NCL-5 (1 ♂), NCL-22 (2 ♂♂, 3 ♀♀), NCL-29 (1 ♂), NCL-139 (1 ♂).

Remarks. This species occurs in an arc from Hawaii westwards through the Carolines to Papua New Guinea, Vanuatu and New Caledonia. It has not yet been found in the south Pacific (Fiji to Society Islands).

Habitat. Amongst red algae, *Sargassum*, epiphytes and coral rubble, 0–2 m.

Distribution. Hawaii, Caroline Islands, Vanuatu, Papua New Guinea, New Caledonia.

Bemlos tui (Myers)

Fig. 5b

Lembos tui Myers, 1985c: 398, figs. 255–258.
Bemlos tui.–Myers, 1995: 30, fig. 3.

Material examined. NCL-27 (3 ♂♂, 2 ♀♀).

Remarks. New Caledonian material differs from type material in the strong deflection of the robust posterodistal tooth of the male gnathopod 1 propodus. In other respects it closely resembles specimens from both Samoa and Papua New Guinea.

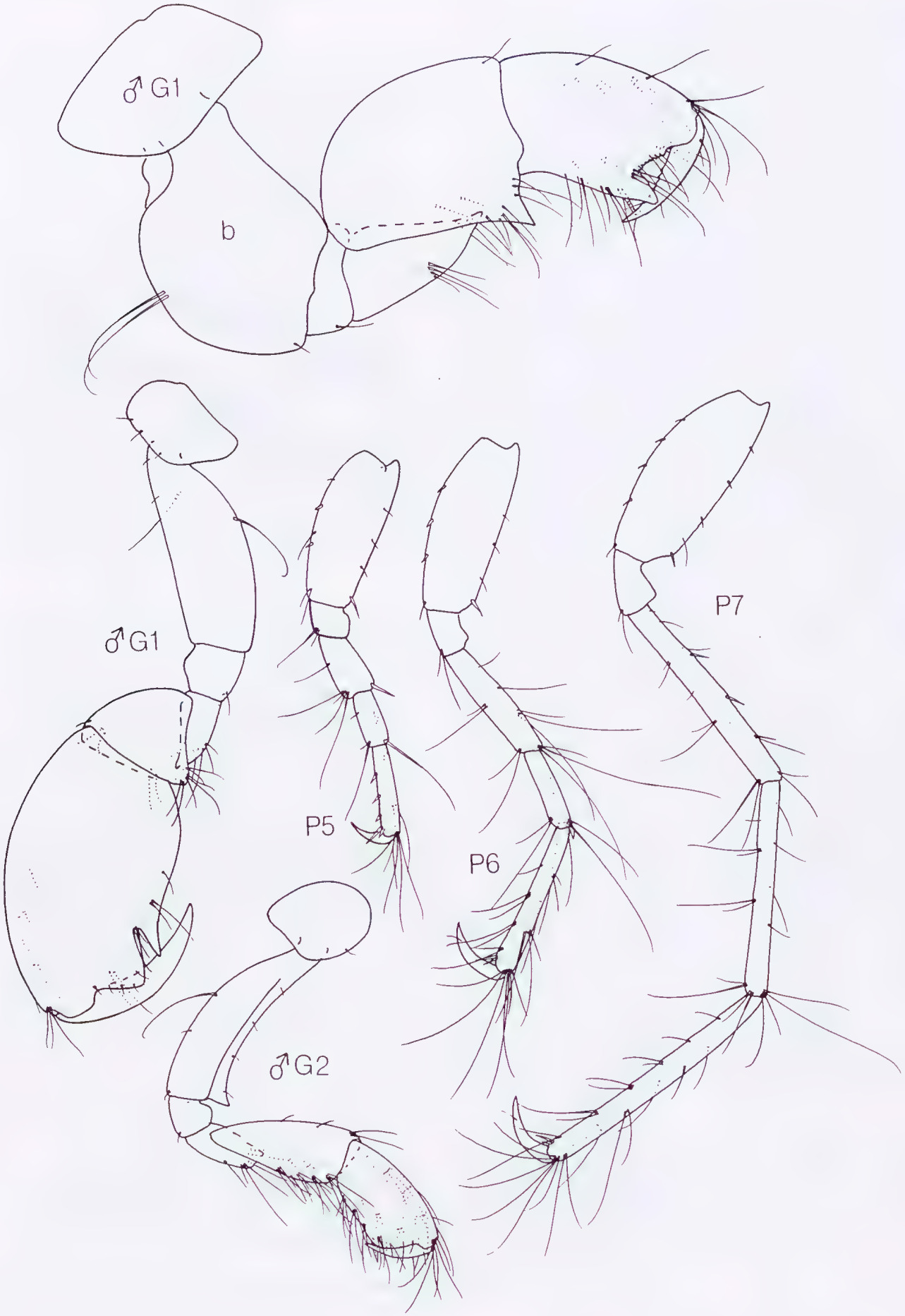

Figure 5. *Bemlos saloteae* (Myers). Pointe de Easo, Baie de Santal, Lifou, Loyalty Islands, NCL-235; *Bemlos tui* (Myers) (b) off Ilot Maitre, Noumea Lagoon, New Caledonia, NCL-27.

Habitat. In *Cymodocea* spp., 0.3 m.

Distribution. Western Samoa, Papua New Guinea, New Caledonia.

Bemlos saloteae (Myers, 1985c)

Fig. 5

Lembos saloteae Myers, 1985c: 373, figs. 238–241.–Myers, 1986: 271, 288.
Bemlos saloteae.–Myers, 1988a: 188.–Myers, 1988b: 284, figs. 15–16.

Material examined. NCL-231 (1 ♂, 1 ♀, 1 immature), NCL-234 (1 ♂), NCL-235 (2 ♂♂, 2 ♀♀), NCL-238 (1 ♀).

Remarks. Loyalty Island material is similar to that described from Tonga and Queensland except that the present material is of much more slender proportions, with elongate appendages, particularly pereopods 6 and 7.

Habitat. Amongst *Halimeda* and red algae, 2–18 m.

Distribution. Tonga, Queensland, Loyalty Islands.

Globosolembos Myers

Globosolembos excavatus (Myers)

Lembos excavatus Myers, 1975: 32, figs. 76–82.–Ledoyer, 1982: 218, figs. 104–105 (in part).
Lembos processifer.–Ledoyer, 1984: 35 (in part), fig. 16 ("forme 2") (not *L. processifer* Pirlot, 1938: 330, figs. 147–149).
Lembos (Globosolembos) excavatus Myers, 1985a: 363, fig 234.
Globosolembos excavatus.–Myers, 1986: 285, figs. 11–12.–Myers, 1988b: 329.

Material examined. NCL-7 (1 ♂, 6 ♀♀), NCL-22 (1 ♂, 1 ♀), NCL-27 (1 ♀), NCL-139 (1 ♂, 1 ♀), NCL-199 (1 ♀), NCL-209 (1 ♂).

Habitat. In coral rubble, *Cymodocea* spp. and mixed algae, 0–27 m.

Distribution. East Africa, Madagascar, north-eastern Australia, New Caledonia, Tonga.

Globosolembos clavicornis n.sp.

Figs. 6–7

Type material. HOLOTYPE male, 2.5 mm, AM P52758, Grand Recif Mbere, 22°19.90'S 166°13.24'E, steep slope, coarse rubble, 10–12 m depth, J.K. Lowry, 21 November 1995, NCL-156. PARATYPES, 10 ♂♂, 9 ♀♀, 4 immature, AM P52759, NCL-156.

Diagnosis. Male 2.5 mm, female 2.8 mm. Male pereon lacking sternal processes. Head lateral lobes only moderately produced; eye moderately large situated proximal to lobes; distoventral margin poorly recessed, moderately deep. Antenna 1 a little shorter than body length; peduncular articles in the basi-distal length ratios 7:9:3; articles 2–3 ventral margin with long stout setae; accessory flagellum composed of one long and one rudimentary terminal article; primary flagellum article 1 ventral margin with a few long stout setae, remaining articles poorly setiferous; flagellum longer than peduncle, with about 15 articles. Antenna 2 robust, subpediform, about one half length of antenna 1; peduncular articles 4 and 5 subequal in length, but article 4 distinctly broader, both articles strongly setiferous, the ventral margins with long, stout setae; flagellum shorter than peduncular article 5, with 6 articles, each with a long ventrodistal strong seta. Mouthparts of typical *Globosolembos* structure; mandible palp article 3 shorter than 2, subovoid, posterior margin with a few long marginal setae and an understory of short, stout setae. Male gnathopod 1 weakly setiferous; coxa produced forward, rounded; basis stout, excavate on anterior outer face for reception of carpus when folded; carpus subtriangular, cup-shaped, about as broad as long; propodus subround, palm evenly convex, defined by an obtuse angle and a strong seta; dactylus strong, falcate. Female gnathopod 1 similar to that of male, but palm sinuous, produced into a right angle. Gnathopod 2 coxa subrectangular, rounded; basis elongate, anterior margin weakly concave; carpus subtriangular, nearly twice as long as broad; propodus subrectangular, subequal in length with carpus, palm oblique, evenly convex, defined by a stout seta; dactylus short. Pereopods 3–4 dactylus about two-thirds length of propodus. Pereopods 5–7 in the length ratios 3:4:6. Epimera posteroventral corner rounded; epimera 1–2 with a few plumose setae on the ventral margin. Uropod 1 peduncle longer than outer ramus and with strong distoventral spine, one half length of peduncle; inner ramus a little longer than outer, each ramus with a single marginal stout seta. Uropod 2 peduncle shorter than inner ramus and with strong distoventral spine, over one half length of peduncle; inner ramus distinctly longer than outer, each ramus with a single marginal stout seta. Uropod 3 rami very reduced and shorter than peduncle, subequal in length, lacking marginal setae, but with long terminal setae. Telson dorsolateral crests each with a pair of unequal slender setae.

Ovigerous females with 1–2 eggs.

Remarks. In its diminutive size, short article three of the mandibular palp and reduced uropod 3 rami, this species resembles *G. tiafaui* Myers from Western Samoa. It differs from that species and indeed from all other known *Globosolembos* species, by the strong stout setae on antenna 2.

Habitat. In coral rubble, 10–12 m.

Distribution. Known only from the type locality.

Etymology. From the Latin *clavus* = spike and *cornus* = horn, referring to the spiky appearance of antenna 2.

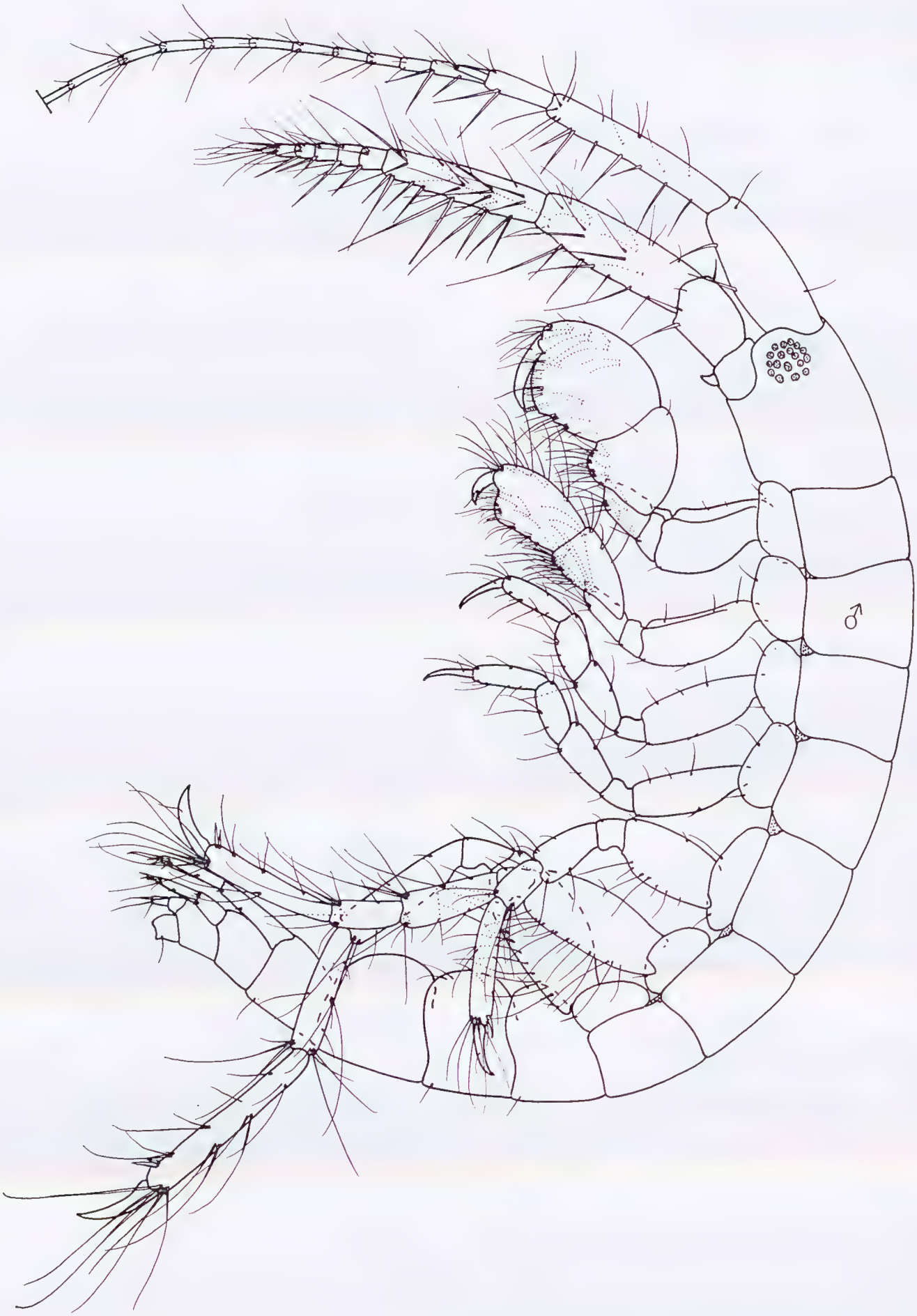

Figure 6. *Globosolembos clavicornis* n.sp. Grand Recif Mbere, Noumea Lagoon, New Caledonia, NCL-156.

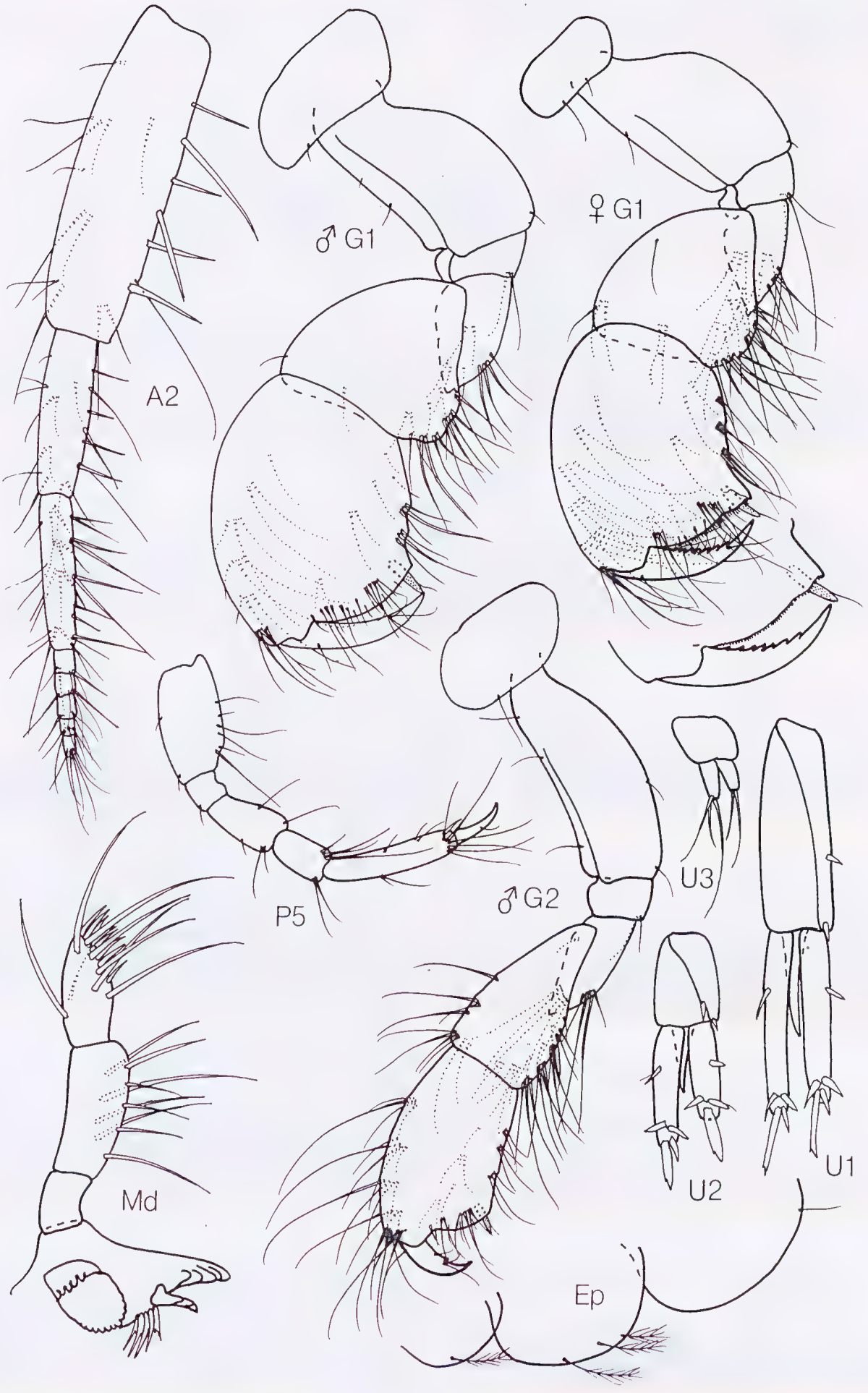

Figure 7. *Globosolembos clavicornis* n.sp. Grand Recif Mbere, Noumea Lagoon, New Caledonia, NCL-156.

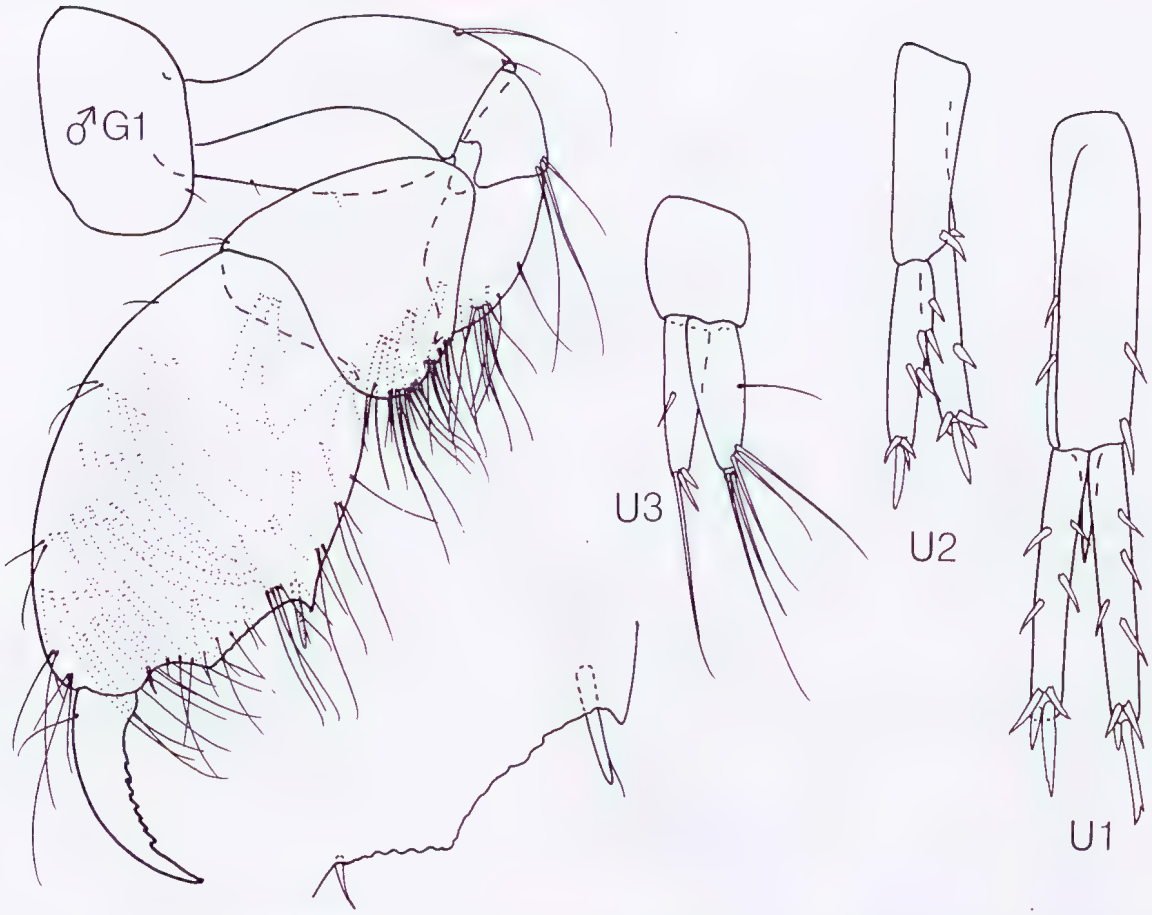

Figure 8. *Globosolembos lunatus* Myers. Grand Recif Mbere, Noumea Lagoon, New Caledonia, NCL-198.

Globosolembos lunatus Myers, 1988b

Fig. 8

Globosolembos lunatus Myers, 1988b: 329, figs. 55–56.

Material examined. NCL-35 (1 ♀), NCL-198 (1 ♂).

Remarks. Material agrees well with the original description of the species from Australia.

Habitat. Amongst *Halimeda* and dead *Acropora* with epiphytes, 20–35 m.

Distribution. Australia (Victoria) and New Caledonia.

Globosolembos forgesi n.sp.

Figs. 9–10

Type material. HOLOTYPE male, 4.0 mm, AM P52760, off Recif To, Passe de Boulari, 22°30.15'S 166°26.43'E, rocks encrusted with lithothamnia, 30 m, ORSTOM divers, 8 November 1995, NCL-45. PARATYPES, 2 ♀♀, AM P52761, NCL-45.

Diagnosis. In life: rear of each pereon segment with thin orange band. Margins of cephalon and base of antenna 1 article 1 also orange banded. Eye large, chocolate brown.

In alcohol (one week): white, eye colourless. Male 4.0 mm, female 4.5 mm. Head lateral lobes only moderately produced; eye moderately large; distoventral margin poorly recessed, moderately deep. Antenna 1 peduncular article 1 longer than head; other articles missing in all specimens. Antenna 2 peduncular articles 4–5 and flagellum missing in all specimens. Mouthparts of typical *Globosolembos* structure; mandible palp article 3 longer than 2, posterior margin weakly falcate, with a few long marginal setae and an understory of short unequal sized setae. Male gnathopod 1 coxa produced forward, rounded; basis stout, excavate on anterior outer face for reception of carpus when folded, anterodistal margin of inner face produced into a rounded spur; carpus subtriangular, cup-shaped, broader than long; propodus subovoid, palm short, defined by a triangular process and lacking a stout seta, posterior margin medially with a strong forward directed spine; dactylus strong, falcate, opposable to medial spine. Female gnathopod 1 similar to that of male, but palm sinuous, produced into a triangular process and lacking a medial spine on the posterior margin. Gnathopod 2 coxa subrectangular, rounded; basis elongate, anterior margin weakly concave; carpus subtriangular, nearly twice as long as broad; propodus subrectangular, subequal in length with carpus, palm oblique, evenly convex; dactylus slightly overlapping palm. Pereopods 3–4 dactylus a little over half length of propodus. Pereopods 5–7 missing in all specimens. Epimera posteroventral corner rounded. Uropod 1 peduncle longer than outer ramus and with strong distoventral spine, less than one half length of peduncle; inner ramus a little longer than outer, each ramus with stout marginal setae. Uropod 2 peduncle shorter than

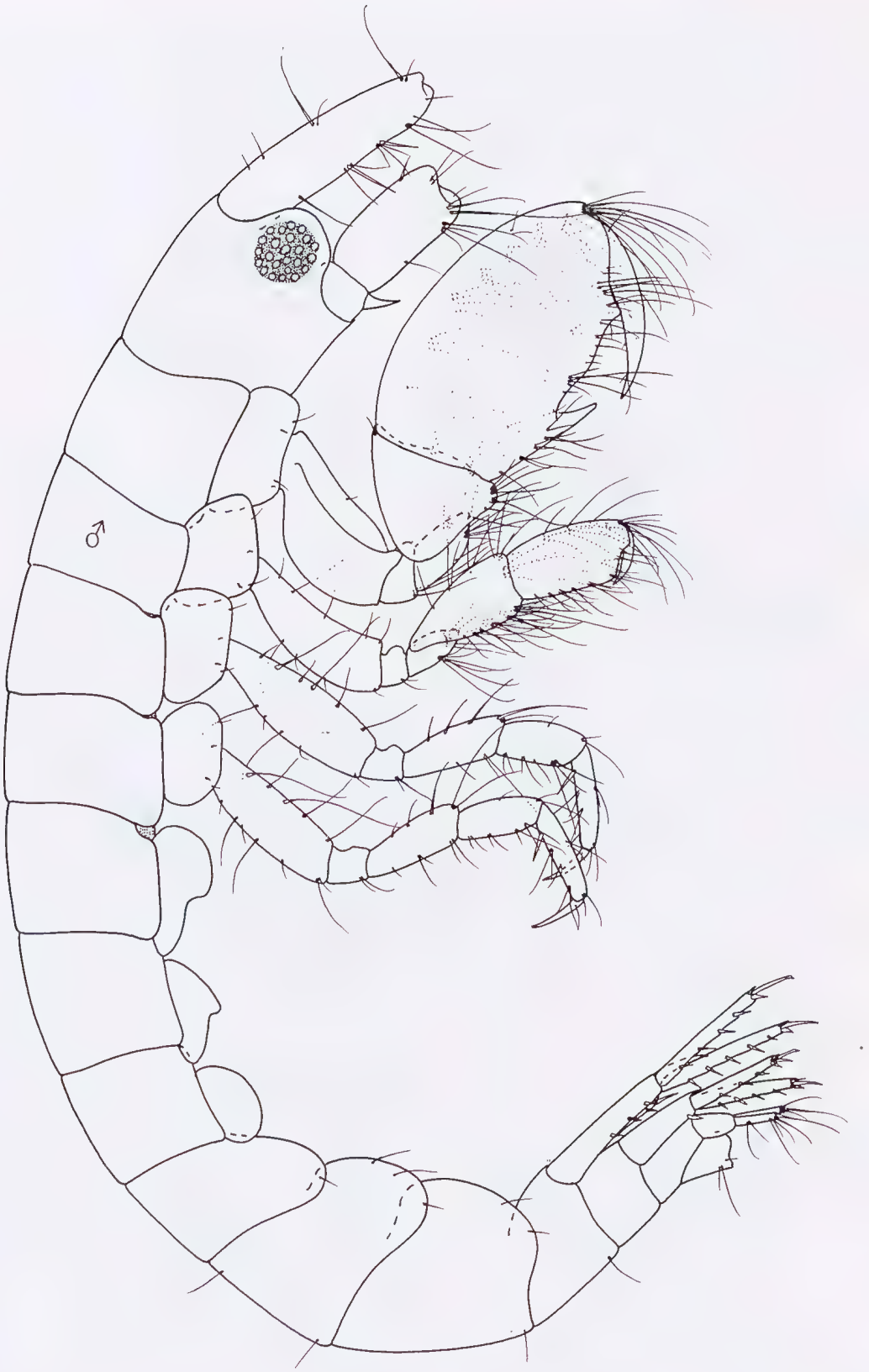

Figure 9. *Globosolembos forgesi* n.sp. Off Recif To, Passe de Boulari, Noumea Lagoon, New Caledonia, NCL-45.

inner ramus and with strong distoventral spine, less than one half length of peduncle; inner ramus longer than outer, both rami with many stout marginal setae. Uropod 3 rami longer than peduncle; inner ramus longer than outer, with two marginal strong setae; outer ramus with a small second article and a pair of long marginal setae; both rami with long distal setae. Telson dorsolateral crests each with a pair of unequal slender setae.

Remarks. This species differs from most *Globosolembos* species in the strong posterior marginal spine on the male gnathopod 1 propodus. In this respect it resembles males

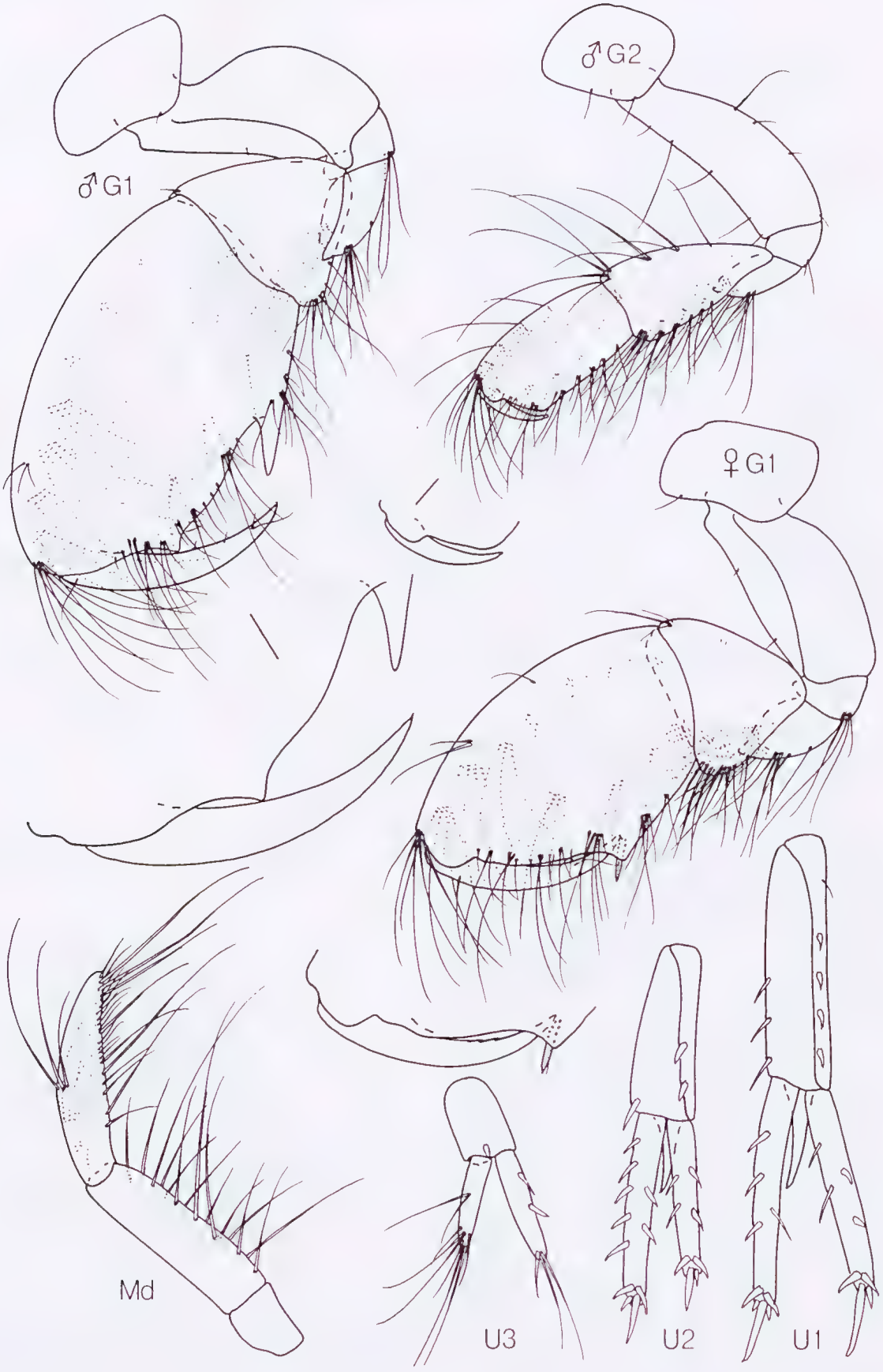

Figure 10. *Globosolembos forgesi* n.sp. Off Recif To, Passe de Boulari, Noumea Lagoon, New Caledonia, NCL-45.

of species in genera such as *Bemlos, Protolembos* and others. However, that this is a homoplasy can be seen by the weak sexual dimorphism of the gnathopoda and the mandible palp article 3 shape (elongate, weakly falcate) and setation (unequal sized understory of short setae on posterior margin) which are diagnostic characters of *Globosolembos*. The male gnathopod 1 resembles that of *Globosolembos excavatus* in general shape, differing only

in the development of a medial tooth. In *Bemlos* and *Protolembos* the tooth develops in young males as a small excavation in the palm. This excavation deepens and in some species the tooth then migrates to a more medial position. Unfortunately juveniles of *G. forgesi* are not available for examination, but it is anticipated that the tooth may develop differently in this species, since it appears to be a secondary rather than primary feature.

Habitat. On rocks encrusted with lithothamnia, 30 m.

Distribution. Known only from the type locality.

Etymology. Named after the carcinologist Dr Bertrand Richer de Forges of ORSTOM.

Grandidierella Coutière

Grandidierella kanakensis n.sp.

Figs. 11–12

Type material. HOLOTYPE male 3.2 mm, AM P52762, off Ilot Maitre, 22°20.50'S 166°24.40'E, *Cymodocea*, 0.3 m, A.A. Myers, 6 November 1995, NCL-27.

Diagnosis. Male, 3.2 mm. Pereon lacking sternal processes. Head lateral lobes scarcely produced; eye moderately large; distoventral margin poorly recessed. Antenna 1 three quarters body length; peduncular articles in the basi-distal length ratios 7:9:3; accessory flagellum composed of a single article about one third length of flagellar article 1; flagellum longer than peduncle with 14 articles, the terminal article rudimentary, articles 4, 6 and 8–13 with aesthetascs. Antenna 2 robust, sub-pediform, subequal in length with antenna 1; peduncular articles 4 and 5 subequal; flagellum a little shorter than peduncular article 5, with 6 articles, articles 4–6 with stout ventral setae. Mouthparts not dissected. Male gnathopod 1 basis very enlarged, subovoid, weakly setiferous; carpus massive, subovoid, weakly setiferous, with a strong forward projecting spine on the inner face, close to the posteroproximal margin and with a similar strong spine on the posterodistal margin; propodus much less than half length and breadth of carpus, palm obsolescent; dactylus stout, three quarters length of propodus, ventral margin with three strong teeth. Gnathopod 2 basis flask-shaped, anterior margin with irregular flange; carpus subtriangular, anterior margin with a brush of very long setae; propodus subrectangular three quarters length of carpus, but less than half its width, palm oblique, weakly convex; dactylus strong, slightly overlapping palm. Pereopods 3–4 basis anterior margin weakly convex; dactylus a little shorter than propodus. Pereopods 5–7 in the length ratios 6:9:11; pereopod 7 basis posterior margin with a few long pectinate setae. Epimera 1–3 rounded, each with a small distoventral seta. Uropod 1 peduncle longer than rami, with a small interramal spine, one sixth length of peduncle; rami subequal. Uropod 2 peduncle shorter than rami, lacking an interramal spine; inner ramus longer than outer. Uropod 3 uniramous; peduncle short less than one quarter length of slender ramus. Telson dorsolateral crests each with a pair of unequal slender setae.

Female unknown.

Remarks. This species is similar to *G. bispinosa* Schellenberg, but differs in the structure of the male gnathopoda. Gnathopod 1 carpus has a strong posteroproximal spine and lacks a spine on the inner medial face and the stout dactylus bears very strong teeth. Gnathopod 2 has the carpus sub-triangular, the propodus only two thirds the length and two thirds the breadth of the carpus.

Ledoyer (1984) described a single male specimen of *Grandidierella* from the same locality and habitat as the present material, under the name *G. bispinosa* Schellenberg. He did not describe or figure a posteroproximal spine on the male gnathopod 1 carpus, or note deep toothing on the dactylus. In addition, the male gnathopod 2 is figured as subequal with the carpus and the carpus is sub-ovoid. Ledoyer's material was of a similar size to present material. Its synonymy remains unresolved.

Habitat. Amongst *Cymodocea* in 0.3 m.

Distribution. Known only from the type locality.

Etymology. After the country of origin—Kanaky (New Caledonia).

Orstomia n.gen.

Diagnosis. Mandible palp article 3 shorter than article 2, falcate; labium mandibular projections elongate, acute; anterior coxae overlapping or contiguous, posterior coxae disjunct; male gnathopod 1 larger than gnathopod 2, carpochelate; male gnathopod 2 subchelate; pereopods 3–4 ordinary; epimeron 3 posterior margin rounded; urosomites 1–3 free; uropods 1–2 biramous, rami well developed; uropod 3 uniramous without hooks or denticles.

Included species. *Orstomia kanakia* (monotypy).

Etymology. After the Organisation de Recherche Scientifique Territoire Outre-Mer.

Orstomia kanakia n.sp.

Figs. 13–14

Type Material. HOLOTYPE male, 2.4 mm, AM P52763, outer face, Grand Recif Mbere, 22°19.90'S 166°13.24'E, human dredge on coarse carbonaceous sand bottom, 64 m, ORSTOM diver, P. Hamel, 23 November 1995, NCL-185. PARATYPES, NCL-185 (2 ♂♂, 2 ♀♀), AM P52764.

Diagnosis. Male and female to 2.5 mm. Male pereon segments 3–6 with sternal processes, spiniform on segments 3–4, laminar on segments 5–6. Head lateral lobes only moderately produced; eye large with only a few scattered ommatidia, situated proximal to the lobes; distoventral margin poorly recessed, shallow. Antenna 1 and 2 unknown. Labrum rounded, distally setose. Mandible molar triturative, spine row of four spines; palp article 3 shorter than article 2, falcate, distal half of posterior margin with a row of short setae bordered distally and proximally by a few long setae. Maxilla 1 inner plate with a single long seta; palp longer than outer plate with 6 distal stout setae. maxilla 2 inner plate, inner face with oblique row

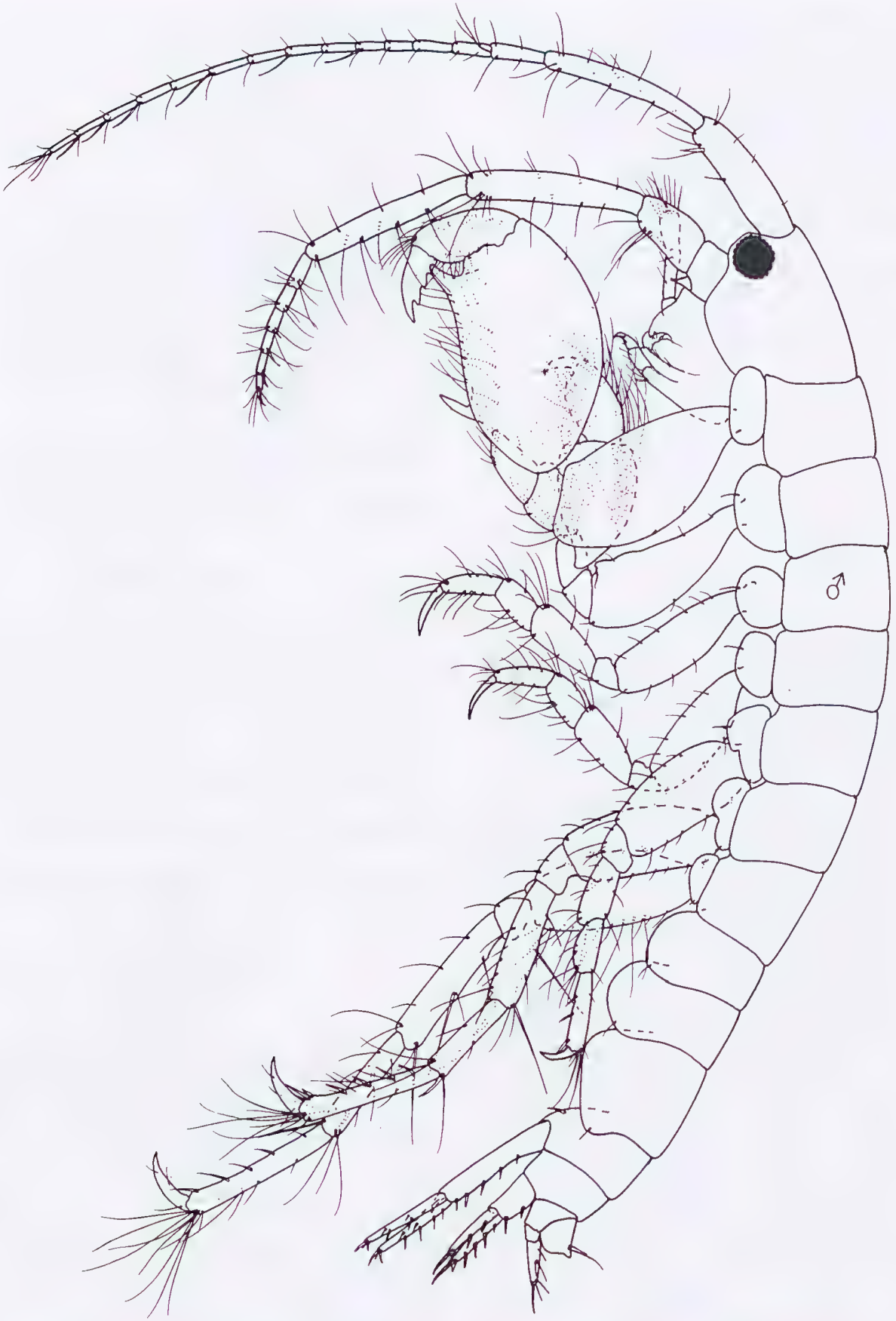

Figure 11. *Grandidierella kanakensis* n.sp. Off Ilot Maitre, Noumea Lagoon, New Caledonia, NCL-27.

of setae. Labium mandibular processes elongate, acute. Maxilliped palp of typical aorid form. Male gnathopod 1 weakly setiferous; coxa subsquare, anterodistal margin not produced; basis swollen, anterior margin excavate for reception of carpus when folded; carpus greatly enlarged, subovoid, posterodistal margin produced into a triangular, forward projecting tooth; propodus one half length and less than one half breadth of carpus, posterior margin with strong, acute medial tooth, palm short, transverse; dactylus stout, three quarters length of propodus, posterior margin

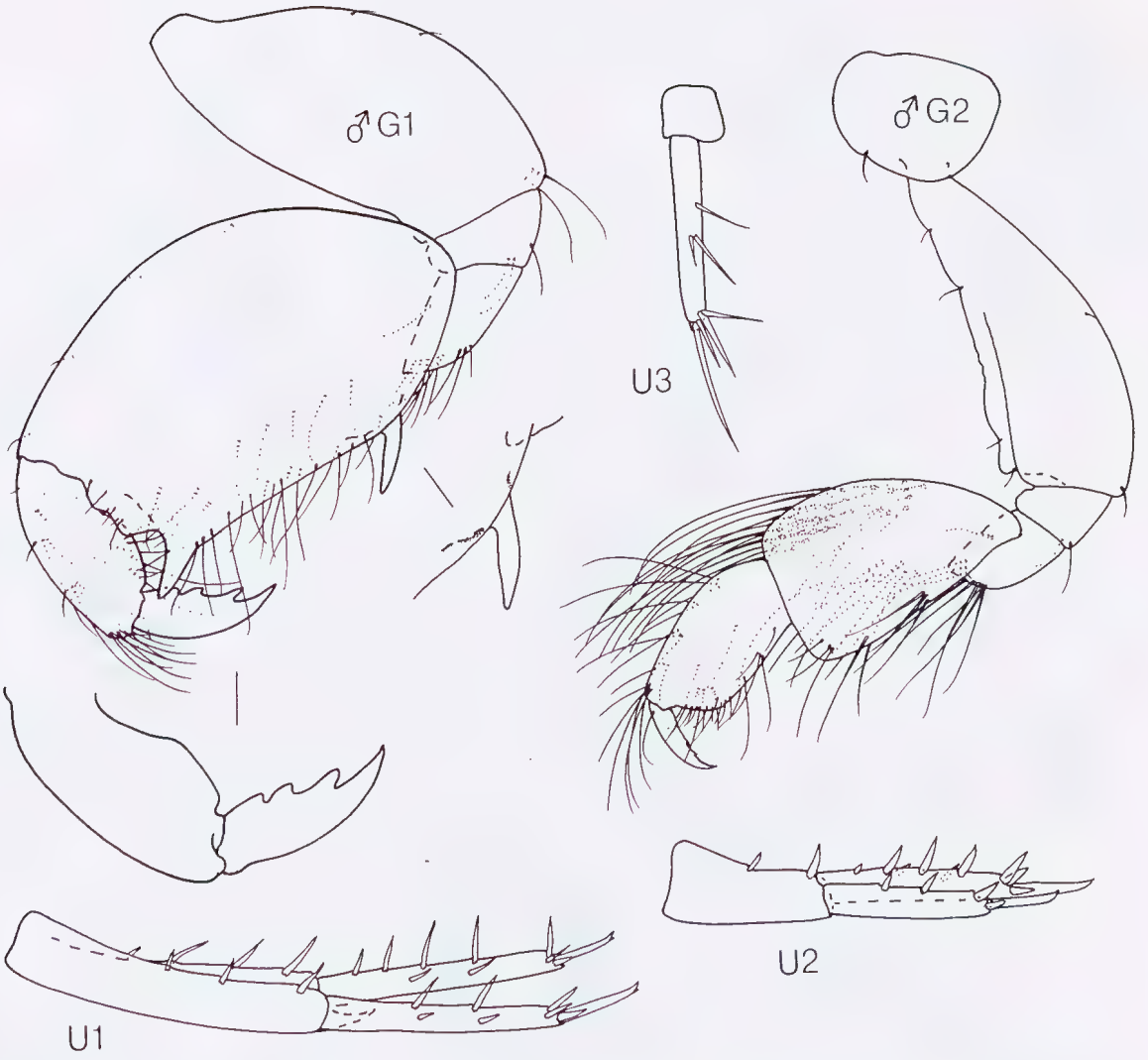

Figure 12. *Grandidierella kanakensis* n.sp. Off Ilot Maitre, Noumea Lagoon, New Caledonia, NCL-27.

with strong, subdistal spine. Female gnathopod 1 slender; coxa subrectangular; basis slender; carpus and propodus slender; propodus two thirds length of carpus, with small, acute palmar spine, proximal to which is a stout seta; dactylus stout, ventral margin with three spines. Male gnathopod 2 basis anterior margin strongly concave, posterior margin strongly convex; carpus slender, more than five times as long as broad; propodus a little narrower than and half length of carpus, palm oblique almost obsolescent, defined by a stout seta; dactylus short, stout, a little over half length of propodus. Female gnathopod 2 similar to that of male, but basis anterior and posterior margins substraight; carpus only a little over twice as long as broad. Pereopods 3–4 slender; dactylus half length of propodus. Pereopods 5–7 unknown. Epimera 1–3 rounded, each with a small posteroventral seta. Uropod 1 peduncle shorter than rami with a distoventral interramal spine about one third length of peduncle; rami slender, subequal, with a few stout marginal setae. Uropod 2 peduncle much shorter than rami, with a distoventral interramal spine about one half length of peduncle; rami slender, outer ramus the longer, with a few stout marginal setae. Uropod 3 uniramous, ramus one and one half times length of peduncle, with four long distal setae, but lacking marginal setae. Telson with weak dorsolateral crests, each bearing a single long seta and three short setae.

Remarks. The falcate madibular palp, maxilla 1 inner plate with single long seta and elongate, acute mandibular projections of the labium are all typical aorid mouthpart features. The enlarged, dominant gnathopod 1 and sternal processes of the male are also characteristic of aorids. In the carpochelate male gnathopod 1 it resembles *Microdeutopus* and *Ericthonius* but differs from the former in its uniramous uropod 3 and from the latter in lacking a hooked uropod 3. It most closely resembles the north Atlantic genus *Chevreuxius* Bonnier, but differs in having a fully biramous uropod 2 and in having mandibular palp article 3 shorter than article 2 and falcate.

Habitat. On a sand bottom, 64 m depth.

Distribution. Known only from the type locality.

Etymology. After the Kanaks, the indigenous peoples of New Caledonia.

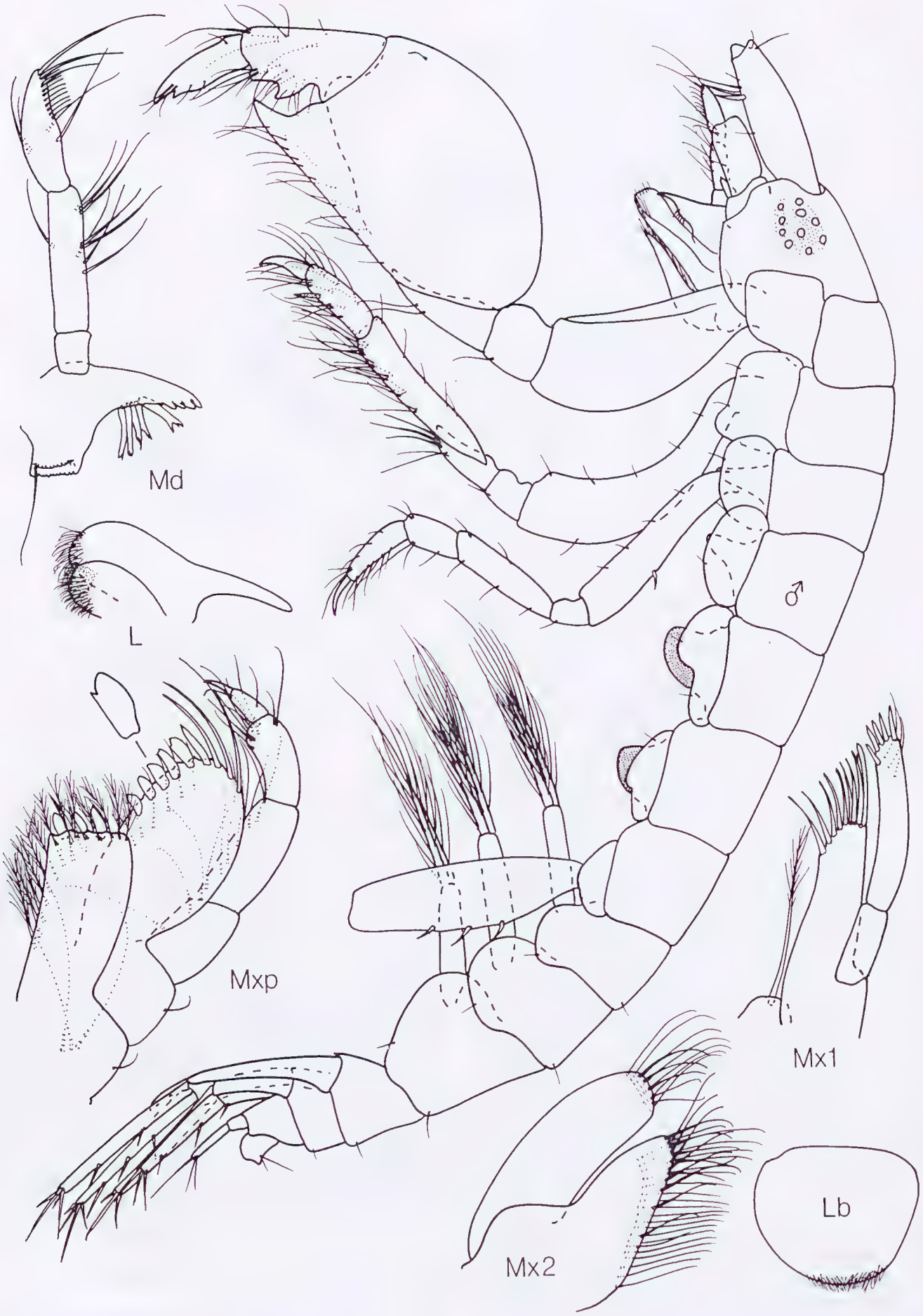

Figure 13. *Orstomia kanakia* n.sp. Outer face, Grand recif Mbere, Noumea Lagoon, New Caledonia, NCL-185.

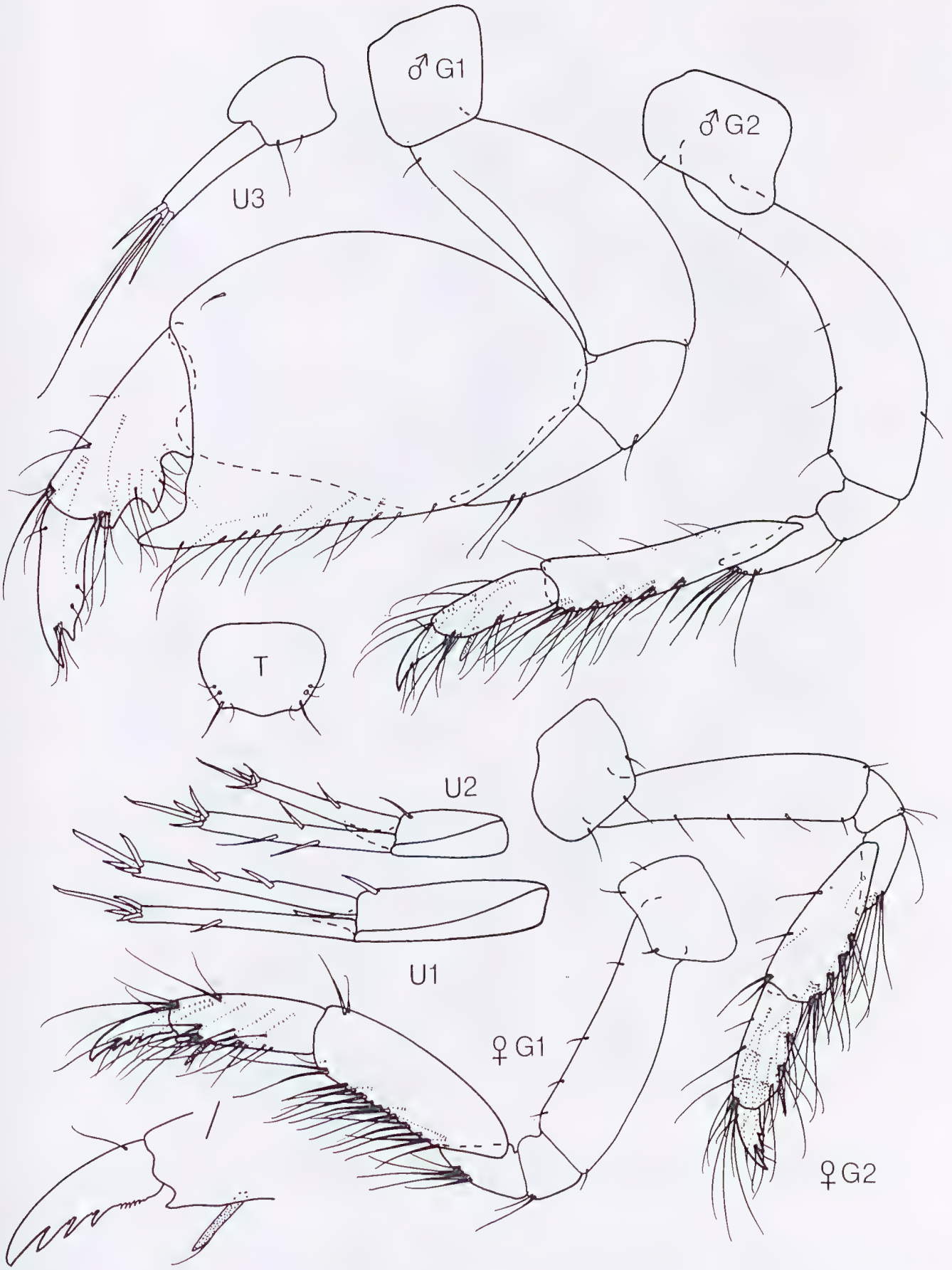

Figure 14. *Orstomia kanakia* n.sp. Outer face, Grand recif Mbere, Noumea Lagoon, New Caledonia, NCL-185.

Figure 15. *Protolembos crouyensis* n.sp. Midway between Ilot des Goelands and Grand Recif d'Abore, Noumea Lagoon, New Caledonia, NCL-116.

Protolembos Myers

***Protolembos crouyensis* n.sp.**

Figs. 15–16

Lembos sp. Ledoyer, 1984: 39, fig 13B.

Type material. HOLOTYPE male, 2.3 mm, AM P52765, midway between Ilot des Goelands and Grand Recif d'Abore, 22°24.10'S 166°20.90'E, *Halimeda* with small leaves, 10 m, ORSTOM divers, Pascal Hamel, 16 November 1995, NCL-116. PARATYPES, 3 ♂♂, 4 ♀♀, AM P52766, NCL-116.

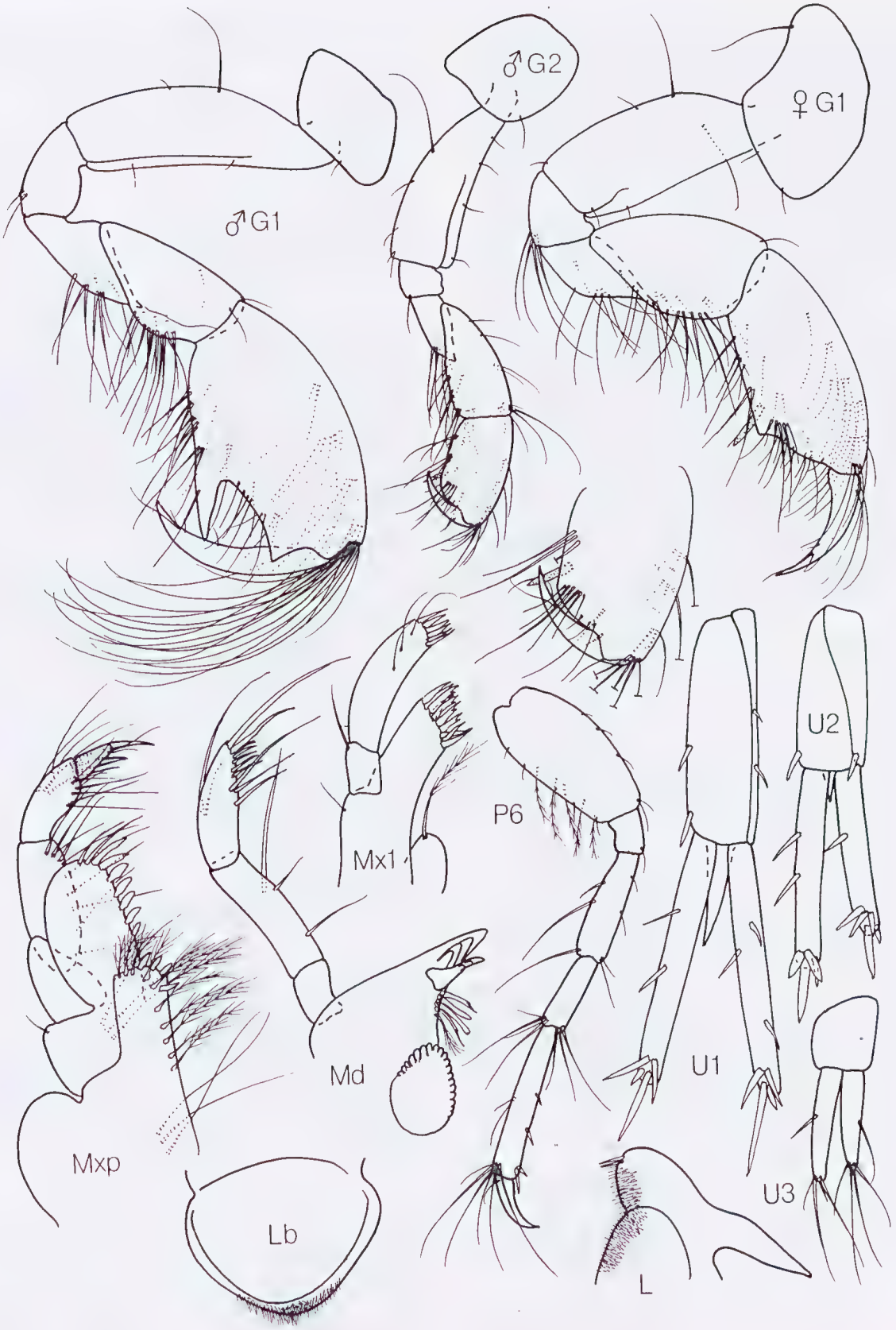

Figure 16. *Protolembos crouyensis* n.sp. Midway between Ilot des Goelands and Grand Recif d'Abore, Noumea Lagoon, New Caledonia, NCL-116.

Other material examined. NCL-68 (2 ♀♀), NCL-111 (2 ♂♂, 2 ♀♀).

Diagnosis. Body, especially pereon, epimera, coxae and pereopod 5–7 bases speckled with dark brown (in alcohol) pigment. Head lateral lobes only moderately produced; eye moderately large situated proximal to lobes; distoventral margin poorly recessed, moderately deep. Antenna 1 about one half body length, weakly setiferous; peduncular articles in the basi-distal length ratios 12:14:5; accessory flagellum with 4 articles, the terminal article rudimentary; primary flagellum subequal in length with peduncle, with about 10 articles. Antenna 2 only moderately stout, about two thirds length of antenna 1,

weakly setiferous; peduncular articles 4 and 5 subequal in length; flagellum shorter than peduncular article 5, with 4 articles, articles 2–4 each with a ventrodistal strong seta. Mouthparts of typical *Protolembos* structure, but mandible palp article 3 a little shorter than article 2, subovoid, posterior margin with a few long marginal setae and an understory of short, equal length, stout setae. Maxilliped peduncle article 1 with rounded wing-like process on anterior margin. Male gnathopod 1, coxa produced forward, rounded; basis relatively slender; ischium and merus relatively long; carpus subtriangular, a little less than twice as long as broad; propodus large, one and one half times as long as broad, narrow proximally, broad distally, palm short transverse, ending in an acute point, followed by a deep triangular excavation, bordered by a strong, acute ending, posterior marginal tooth, inner face of anterior margin of propodus clothed distally in very long setae; dactylus strong, falcate, greatly overlapping palm and also overlapping marginal tooth. Female gnathopod 1 coxa subrectangular, deeper than broad; basis moderately stout; carpus triangular, about one and one half times as long as broad; propodus subrectangular, about twice as long as broad, palm oblique, sinuous, terminating in a right angle and defined by a stout seta; dactylus stout, overlapping palm. Gnathopod 2 coxa subrectangular, rounded; basis moderately stout, anterior margin weakly concave, carpus subtriangular, nearly twice as long as broad; propodus subrectangular, a little shorter than carpus, palm oblique, evenly convex, defined by a stout seta; dactylus overlapping palm. Pereopods 3–4 dactylus over two-thirds length of propodus. Pereopods 5–7 in the length ratios 6:9:14. Epimera posteroventral corner rounded. Uropod 1 peduncle shorter than outer ramus and with strong distoventral spine, less than half length of peduncle; rami subequal, each ramus with a few marginal stout setae. Uropod 2 peduncle shorter than inner ramus and with triangular distoventral spine, about one seventh length of peduncle; inner ramus distinctly longer than outer, with two marginal stout setae; outer ramus with one marginal stout seta. Uropod 3 rami longer than peduncle; inner ramus longer than outer, each ramus with a slender marginal seta and a group of long slender terminal setae; outer ramus lacking second article. Telson dorsolateral crests each with a pair of unequal slender setae.

Remarks. This species is closest to *P. kidoli* (Myers) from Tanzania and *P. murrarum* Myers from New South Wales, Australia. It differs from both these species in the weakly setiferous male gnathopod 2 and in the short article 3 of the mandible palp. It differs from *P. kidoli* also in the lack of a spine on the palm of the male gnathopod 2. In having article 3 of the mandible palp shorter than article 2 it resembles species of *Meridiolembos*, but those species lack a wing-like process on the anterior margin of article 1 of the maxilliped.

Habitat. Amongst *Halimeda, Sargassum* and fine red alga, 10–20 m.

Distribution. Not currently known outside New Caledonia.

Etymology. Named after the island of Crouy close to the type locality.

Xenocheira Chevreux

Xenocheira sp.

Xenocheira seurati Ledoyer, 1984, 41, fig. 19.
Xenocheira ?seurati Moore, 1988: 712, figs. 4–7.

Material examined. NCL-210 (3 ♂♂, 9 ♀♀, 2 immature), NCL-219 (5 ♀♀).

Remarks. Present material agrees well with that described by Moore from Western Australia and by Ledoyer (1984), from New Caledonia. *Xenocheira seurati* was originally described from the Gambier archipelago by Chevreux (1907, 1908). Moore (1988), examined type specimens of *X. seurati*, but in part due to the age of the material, was unable to convince himself that Australian and New Caledonian material was definitely conspecific with Gambier material. He listed several differences between his material and the types and noted the characteristic shape of the pereopod 5 basis, which is very apparent also in our material. Unfortunately type material is missing this appendage.

Schellenberg (1938) recorded a single female specimen, which he attributed to *Xenocheira seurati*, from Viti Levu, Fiji. As he provided neither description nor figures, this record remains enigmatic. For the present, we assign our material to the unnamed taxon from Australia and New Caledonia, whilst acknowledging that this taxon may later be shown to be synonymous with *X. seurati* Chevreux.

Lyons & Myers (1990) considered *Xenocheira* to be polyphyletic and transferred *X. fasciata* Haswell to *Bemlos* Shoemaker and *X. angusticarpa* Ledoyer to *Lemboides* Stebbing. Thus *Xenocheira* now includes 2–3 known species: *X. seurati* Chevreux, *X.? seurati* and *X. pirloti* Moore.

Habitat. *Dictyota* on dead *Acropora* and soft mud, 20 m.

Distribution. Western Australia and New Caledonia.

Acknowledgments. I am grateful to Dr Bertrand Richer de Forges for all his help and hospitality in New Caledonia, and to all the ORSTOM staff, especially Jean-Louis Menou, Georges Bargibant, Pascal Hamel and Stéphane Bujan for their assistance in sample collection. The work forms part of a larger survey on the amphipods of New Caledonia carried out jointly with Drs Jim Lowry and Ichiro Tekeuchi. I thank them both for their comradeship during the field work.

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Station data

NCL-2 Recif Ricaudy, New Caledonia, 22°18.23'S 166°26.15'E, *Padina*, 1.0 m, A.A. Myers, 30 October 1995.

NCL-4 Recif Ricaudy, New Caledonia, 22°18.23'S 166°26.15'E, anastomosing red alga, 1.0 m, A.A. Myers, 30 October 1995.

NCL-5 Recif Ricaudy, New Caledonia, 22°18.23'S 166°26.15'E, rocks covered with fine red algal felt, 0.1 m, A.A. Myers, 30 October 1995.

NCL-7 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, coral rubble, 0.3 m, A.A. Myers, 31 October 1995.

NCL-8 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, *Sargassum*, 0.3 m, A.A. Myers, 31 October 1995.

NCL-9 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, brown branching alga among *Cymodocea*, 0.3 m, A.A. Myers, 31 October 1995.

NCL-10 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, *Halimeda*, 0.3 m, A.A. Myers, 1 November 1995.

NCL-11 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, coral rubble, 0.3 m, A.A. Myers, 1 November 1995.

NCL-12 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, red coralline alga (tbi), 0.3 m, A.A. Myers, 1 November 1995.

NCL-15 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, *Padina*, 0.3 m, A.A. Myers, 1 November 1995.

NCL-17 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, *Syringodium*, 0.3 m, A.A. Myers, 2 November 1995.

NCL-18 Pointe Bagay, Anse Vata, New Caledonia, 22° 18.23'S 166°26.15'E, *Cymodocea*, 1.0 m, A.A. Myers, 2 November 1995.

NCL-19 Recif Ricaudy, New Caledonia, 22°18.77'S 166°26.92'E, *Padina*, 0.5 m, A.A. Myers, 4 November 1995.

NCL-21 Recif Ricaudy, New Caledonia, 22°18.77'S 166°26.92'E, *Sargassum*, 1.0 m, A.A. Myers, 4 November 1995.

NCL-22 Recif Goro, New Caledonia, 22°19.23'S 167° 00.65'E, coral rubble, 0.3 m, A.A. Myers, 5 November 1995.

NCL-25 Recif Goro, New Caledonia, 22°19.23'S 166° 00.65'E, *Padina* covered rocks, 0.3 m, A.A. Myers, 5 November 1995.

NCL-26 Recif Goro, New Caledonia, 22°19.23'S 166° 00.65'E, *Cymodocea*, 0.5 m, A.A. Myers, 5 November 1995.

NCL-27 Ilot Maitre, 22°20.50'S 166°24.40'E, *Cymodocea*, 0.3 m, A.A. Myers, 6 November 1995.

NCL-28 Between Ilot Maitre and Croissant reef, 22°19.70'S 166°23.30'E, New Caledonia, *Sargassum*, 10 m, I. Takeuchi, 6 November 1995.

NCL-29 Recif Goro, New Caledonia, 22°19.23'S 166° 00.65'E, *Sargassum*, 1.0 m, I. Takeuchi, 5 November 1995.

NCL-31 Between Ilot Maitre and Croissant reef, New Caledonia, 22°19.70'S 166°23.30'E, *Halimeda*, 10 m, I. Takeuchi, 6 November 1995.

NCL-33 Off Ilot Maitre, New Caledonia, 22°20.57'S 166°25.43'E, red alga, 23 m, ORSTOM divers, 7 November 1995.

NCL-35 Off Ilot Maitre, New Caledonia, 22°20.57'S 166°25.43'E, dead *Acropora* with epiphytes, 20 m, ORSTOM divers, 7 November 1995.

NCL-40 Off Ilot Maitre, New Caledonia, 22°20.57'S 166°25.43'E, dead coral, 20 m, ORSTOM divers, 7 November 1995.

NCL-45 Off Recif To, Passe de Boulari, New Caledonia, 22°30.15'S 166°26.43'E, stones encrusted with *Lithothamnion*, 30 m, ORSTOM divers, 8 November 1995.

NCL-47 Off Recif To, Passe de Boulari, New Caledonia, 22°30.15'S 166°26.43'E, coral rubble, 13 m, ORSTOM divers, 8 November 1995.

NCL-49 Off Recif To, Passe de Boulari, New Caledonia, 22°30.15'S 166°26.43'E, green alga, 32 m, I. Takeuchi, 8 November 1995.

NCL-60 Off Ilot Maitre, New Caledonia, 22°19.35'S 166°25.85'E, grey sponge, 20 m, I. Takeuchi, 10 November 1995.

NCL-63 Off Ilot Maitre, New Caledonia, 22°19.35'S 166°25.85'E, large yellow sea fans, air lift sample, 21 m, J.K. Lowry, 10 November 1995.

NCL-64 Off Ilot Maitre, New Caledonia, 22°19.35'S 166°25.85'E, large hard coral block and coarse sand, some algae, 21 m, J.K. Lowry, 10 November 1995.

NCL-68 Between Isle Ngé and Sèche Croissant, New Caledonia, 22°19.41'S 166°20.89'E, *Sargassum*, 20 m, I. Takeuchi, 9 November 1995.

NCL-79 Entrance of Baie de Citron, New Caledonia, 22°18.17'S 166°26.07'E, *Sargassum*, 1.5 m, I. Takeuchi, 13 November 1995.

NCL-80 Entrance of Baie de Citron, New Caledonia, 22°18.17'S 166°26.07'E, red algae, 1.5 m, I. Takeuchi, 13 November 1995.

NCL-95 Off Ilot Maitre, New Caledonia, 22°19.61'S 166°24.07'E, from leaf of Seagrass, 10.5 m, I. Takeuchi, 14 November 1995.

NCL-97 Off Ilot Maitre, New Caledonia, 22°19.61'S 166°24.07'E, purple sponge, 10.5 m, ORSTOM divers (coll. Georges Bargibant), 14 November 1995.

NCL-98 Off Ilot Maitre, New Caledonia, 22°19.61'S 166°24.07'E, *Padina*-type alga, 10.5 m, ORSTOM divers (coll. Georges Bargibant), 14 November 1995.

NCL-110 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, fine red filamentous alga on fine white sand bottom, 10 m, J.K. Lowry, 16 November 1995.

NCL-111 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, *Halimeda*, fine red alga, 10 m, J.K. Lowry, 16 November 1995.

NCL-112 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, human dredge on fine sand with patches of algae (maybe bluegreen), 10 m, J.K. Lowry, 16 November 1995.

NCL-113 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, coral rubble, 10 m, J.K. Lowry, 16 November 1995.

NCL-116 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, *Halimeda* with small leaves, 10 m, ORSTOM divers, Pascal Hamel, 16 November 1995.

NCL-128 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, white sands, hydroids and algae, 11 m, I. Takeuchi, 16 November 1995.

NCL-129 Midway between Ilot des Goelands and Grand Recif d'Abore, New Caledonia, 22°24.10'S 166°20.90'E, white sands, *Halimeda*, 11 m, I. Takeuchi, 16 November 1995.

NCL-130 Pointe Bagay, New Caledonia, 22°18.23'S 166° 26.15'E, *Sargassum*, 0.5 m, I. Takeuchi, 18 November 1995.

NCL-139 Poé Plage, New Caledonia, 21°36.41'S 165°22.73'E, 200 m off beach, mixed algae from rocks on white sand, 2 m, J.K. Lowry, 19 November 1995.

NCL-153 Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, steep slope, rubble and red alga, 38 m, J.K. Lowry, 21 November 1995.

NCL-154 Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, steep slope, coarse rubble, 12 to 25 m, J.K. Lowry, 21 November 1995.

NCL-156 Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, coarse sand and rubble from gully, 10 to 12 m, J.K. Lowry, 21 November 1995.

NCL-185 Outer face, Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, human dredge on coarse carbonaceous sand bottom, 64 m, ORSTOM diver, P. Hamel, 23 November 1995.

NCL-198 Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, *Halimeda*, 35 m, J.K. Lowry, 22 November 1995.

NCL-199 Grand Recif Mbere, New Caledonia, 22°19.90'S 166°13.24'E, red alga *Asparagopsis taxiformis*, 27 m, J.K. Lowry, 22 November 1995.

NCL-209 Baie de St. Marie, New Caledonia, 22°18.05'S 166°28.13'E, thick coral rubble, J.K. Lowry, 13 m, 29 November 1995.

NCL-210 Baie de St. Marie, New Caledonia, 22°18.05'S 166°28.13'E, dictyotalean growing on dead *Acropora*, 13 m, J.K. Lowry, 29 November 1995.

NCL-212 Poé Plage, New Caledonia, 200 m off beach, *Sargassum*, 1–2 m, J.K. Lowry, 19 November 1995.

NCL-219 Baie de Dumbéa, New Caledonia, 22°13.38'S 166°22.17'E, soft mud bottom with many small cones, 20 m, J.K. Lowry, 30 November 1995.

NCL-231 Pointe de Easo (= Easho), Baie de Santal, Lifou Loyalty Islands, 20°47.27'S 167°07.34'E, near base of the steep coral reef, red alga, 12 m, I. Takeuchi, 27 November 1995.

NCL-234 Dokin, north coast of Lifou, Loyalty Islands, 20°42.15'S 167°09.90'E, small spot on the surface of the coral reef, red alga, 2 m, I. Takeuchi, 28 November 1995.

NCL-235 Pointe de Easo, Baie de Santal, Lifou, Loyalty Islands, 20°47.27'S 167°07.34'E, red alga and hydroids along the steep coral reef, 8–10 m, I. Takeuchi, 28 November 1995.

NCL-237 Pointe de Easo (= Easho), Baie de Santal, Lifou, Loyalty Islands, 20°47.27'S 167°07.34'E, rock base near the seashore, *Sargassum*, 1 m, I. Takeuchi, 28 November 1995.

NCL-238 Dozip (= Jozip), west coast of Lifou, Loyalty Islands, 20°56.30'S 167°20.85'E, near bottom of coral reef, *Halimeda*, 18 m, I. Takeuchi, 29 November 1995.

NCL-246 Prony Bay, near village, southern New Caledonia, 10 m off from the coast, *Sargassum* sp. covered with red muds, 2 m deep, I. Takeuchi, 26 November 1995.

ORSTOM divers: Jean-Louis Menou, Georges Bargibant, Pascal Hamel and Stéphane Bujan.

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Stentor amethystinus (Protista: Ciliophora: Heterotrichida), A Common Protozoan Member of Fresh-water Plankton in Australia

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ABSTRACT. Large numbers of a brown to violet ciliate can often be seen in freshwater lakes and billabongs in Australia. Uninterpreted records by light microscopy and electron microscopy are provided. The ciliates are identified as *Stentor amethystinus* Leidy, 1880. Despite the abundance of this species, this is a new record for Australia.

Heep, Thomas, Jan Rohozinski, Alastair Simpson & David J. Patterson, 1998. *Stentor amethystinus* (Protista: Ciliophora: Heterotrichida), a common protozoan member of fresh-water plankton in Australia. *Records of the Australian Museum* 50(2): 211–216.

Stentor Oken, 1815 (Oken, 1815) is a widespread and familiar genus of heterotrich ciliates (protozoa). Cells are typically trumpet-shaped and often distinctly coloured; different species being green, black, blue, pink or brown (Foissner & Wölfl, 1994; Kahl, 1932; Tartar, 1961).

A brown species of *Stentor* has been reported as occurring in very large numbers in fresh-water bodies in New South Wales, the Australian Capital Territory and Victoria (Laybourn-Parry *et al.*, 1997). It occurs throughout the year but blooms, which can discolour the water, occur at various times from mid-spring to late autumn. Up to 4200 individuals per litre have been counted, and the organism is argued to make a significant contribution to primary production (Laybourn-Parry *et al.*, 1997). It has also probably been reported as "cf. *Climacostomum*" (Walker & Hillman, 1977).

The aim of this study was to establish the identity of this ciliate. The genus *Stentor* has been reviewed most recently by Foissner & Wölfl (1994) who recognised 19 species. Species distinctions are normally made on the basis of cell shape and size, presence/absence of a mucilagenous sheath, macronuclear form, the number of micronuclei and their location, numbers of kineties and membranelles, pigmentation, presence/absence of symbiotic algae. One study (Nilsson, 1986) has added ultrastructural characteristics to assist in distinguishing species. Brown species

have been observed from America (Leidy, 1880), India (Murthy & Bai, 1974), Africa (Nilsson, 1986), South America (Foissner & Wölfl, 1994; Laybourn-Parry *et al.*, 1997), New Zealand (cited in Laybourn-Parry *et al.*, 1997) and from Europe (Foissner *et al.*, 1992; Schneider, 1992). The brown colour results from the combination of symbiotic green algae and numerous dark plum-coloured pigment granules.

The first description of *Stentor* in Australia was of *S. polymorphus* (Shephard, 1891), Shephard found large numbers in pools in the area of Sandringham, Victoria. Other records of *S. polymorphus* in Australia are provided by Schewiakoff (1893) and Gillies (1915). Other species reported from Australia are: *S. igneus* (Shephard, 1904), *S. roeselii* (Stickland & Stickland, 1895), and several unnamed species (Fielder, 1893; Ingram *et al.*, 1997; Laybourn-Parry *et al.*, 1997; Stickland, 1923).

Materials and methods

Stentor was collected in 1994 from Corin Dam and Lake Burley Griffin, both in the Australian Capital Territory close to Canberra, Googong Dam in New South Wales, in 1996, from Lake Tuggeranong (ACT, Canberra) and from a pond near Camden, south-west of Sydney.

Water samples containing *Stentor* were kept at 5 to 14°C in plastic bottles. Attempts to establish long term cultures of the organism have been unsuccessful. Exposure to temperatures above 23° results in a rapid decrease in the number of individuals. Stocks were maintained for up to three months at 18°C under continuous light.

Live ciliates were used for morphological studies. For some detailed studies, a small drop of 0.01M EGTA and 0.1M MgCl2 was added on a slide to stop movement and prevent contraction. Movement and morphology were documented by video records and black and white photography using a *Leica DM* microscope equipped with a dedicated flash system (Patterson, 1982) The sizes of cells were measured using an ocular micrometer.

To obtain typical cell profiles, groups of about 100 cells were left undisturbed on a dissection microscope for 12 or more hours in the dark.

For electron microscopy, cells were fixed simultaneously with ice cold 2.5% glutaraldehyde and 0.2% osmium tetroxide in 50 mM cacodylate buffer. Cells were washed free of fixative in buffer, collected, and dehydrated through a series of ethanols before embedding in Araldite. Fixed material was sectioned with a diamond knife using a *Reichert Ultracut S* ultramicrotome. Sections were collected on *Pioloform* coated slot grids, carbon coated, and stained with lead citrate and uranyl acetate prior examination using a *Zeiss 902* electron microscope.

Results

The species observed is a brown-coloured ciliate with symbiotic algae (Fig. 1a). It is most usually encountered as a short conical swimming cell (Fig. 1b). Cells from the different collecting sites had similar sizes—with lengths varying from 150–220 µm (mean 188 µm, n = 34) and with widths from 106–150 µm at the peristomial region (mean 128 µm, n = 34). When sedentary, cells either lie on their sides on the substrate or attach to vertical surfaces by their posterior ends when they adopt a slightly more elongate body form. The attachment to the substrate is very slight and swimming is resumed at the slightest disturbance. When the animal is incubated at 25°C in the dark overnight the body becomes more trumpet-shaped and the peristomial bulge is withdrawn slightly. The increase in length is achieved principally a slight extension of the posterior end. Under these conditions on average, only 9% of the cells were attached, 7% were rounded swimming cells and 83% were conical swimming cells. No elongate trumpet forms—typical of most other species of *Stentor*—were observed at any time.

The peristomial region typically adopts a domed appearance, and is surrounded by an adoral zone of about 190 (from 168 to 204, mean 191) membranelles (Figs. 1a,b,c). This adoral zone of membranelles (AZM) makes two clockwise turns leading into the buccal cavity with the cytostome located about the quarter of the way into the cell. There are approximately 29 kineties(24 to 31) in the peristomial region. There are approximately 90–100 longitudinal kineties (50–158) on the cell body. The basal bodies give rise to kinetodesmal (*km*) fibres (Fig. 1d), and there are typically about 5–7 overlapping *km* fibres running alongside the kineties (Figs. 1d, e).

The cells were not able to contract completely, although local contractions were observed. Electron-microscopy confirms the existence of a myonemal system—arranged in the form of a perforated layer—the perforations being penetrated by membrane bound lacunae (Fig. 1f).

There is a single spherical to oval macronucleus measuring on average 44 µm × 38 µm (range: 37.5–53 µm × 30–47 µm) (Fig. 1a). The macronucleus is located approximately 2/3 of the way down the cell. The nucleus is typically surrounded by the pigment granules, and these also cluster around the numerous (10 or more) micronuclei which lie close to the surface of the macronucleus (Fig. 1g).

A single large contractile vacuole is located near the middle of the cell and to the left of the buccal cavity. The interior of the cell contains a large number of symbiotic green algae (Fig. 1a) which are about 4 µm in diameter. Under illuminated conditions these are mostly found near the cell surface and aligned along the kineties. There are a large number of small dark pigment granules (<1 µm in diameter), mostly occurring in 4–5 rows between kineties, in the vicinity of the AZM, and also throughout the cytoplasm. (Fig. 1c). These are a dark burgundy colour, and together with the symbiotic green algae give the animal its dark brown, plum or black colour.

When swimming, *Stentor* describes a spiral path with a clockwise rotation when viewed from the front. The axis of rotation can be described by a line drawn from the posterior tip through the middle of the dorsal surface opposite the buccal cavity.

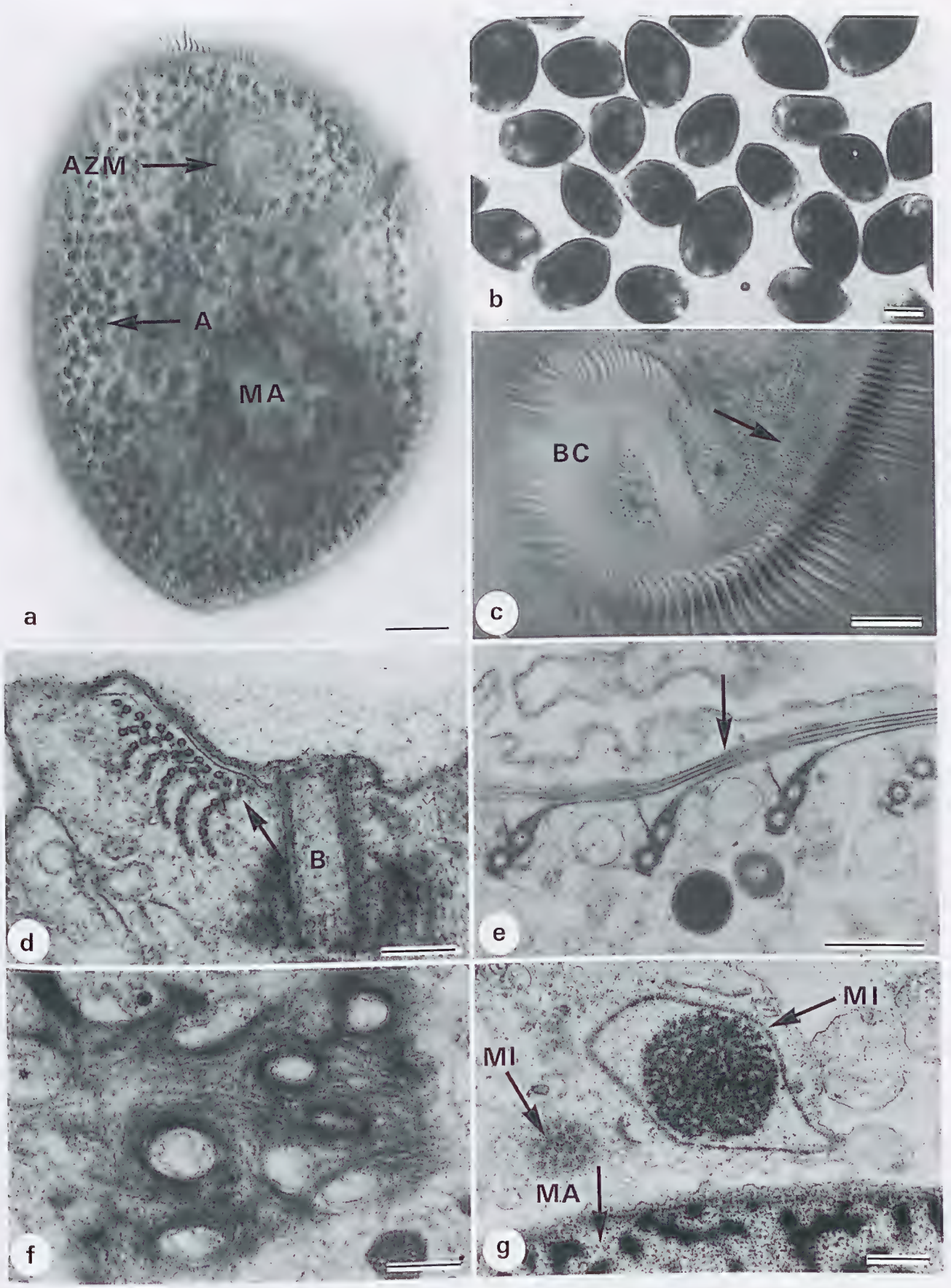

Figure 1. *Stentor amethystinus*. **a**, Ventral view of living cell showing adoral zone of membranelles (AZM), macronucleus (MA) and symbiotic green algae (A), DIC, scale bar 20 µm. **b**, Typical conical forms of living cells, bright-field, scale bar 80 µm. **c**, AZM leading in the buccal cavity (BC), pigment granules (arrow), DIC, scale bar 8 µm. **d**, Electron-micrograph of basal body (B) with associated microtubules of the kinetodesmal fibres in cross section (arrow), scale bar 0.2 µm. **e**, Electron-micrograph showing kintodesmal fibres (arrow) in longitudinal section arising from the basal bodies, scale bar 1 µm. **f**, Electron-micrograph of myonemal system, scale bar 1 µm. **g**, Electron-micrograph of the border of macronucleus(MA) and two mircronuclei (MI). The nucleus to the left has been sectioned through the nuclear envelope and shows the nuclear pores, while that on the right has been sectioned through its centre, scale bar 0.5 µm.

Discussion

The genus *Stentor* is characterised as a genus of contractile and trumpet-shaped heterotrich ciliates, with longitudinal kineties, posterior holdfast, an anterior adoral zone of membranelles (AZM) following a clockwise spiral when seen from above, and no undulating membrane (Kahl, 1932; Tartar 1961). The cells observed by us have these features and are assignable to the genus *Stentor*.

The only members of the genus which have a brown colour are: *S. amethystinus* Leidy 1880 (in Anonymous, 1880); *S. andreseni* Nilsson, 1986; *S. fuliginosus* Forbes, 1891; *S. igneus* Ehrenberg, 1838; *S. niger* (Müller, 1773) Ehrenberg, 1831; and *S. tartari* Murthy & Bai, 1974. *Stentor andreseni* has been synonymized with *S. tartari* (Foissner & Wölfl, 1994).

Stentor tartari is a binucleate species (Murthy & Bai, 1974; Nilsson, 1986). The Australian isolates can be distinguished from this species on the basis of the nuclei alone. Nilsson (1986) used ultrastructural characteristics to add additional characters which distinguish *S. tartari* and *S. amethystinus*. Given the uncertainty over the identity of *S. amethystinus* (see below), we also obtained ultrastructural characteristics. As in Nilsson's *S. amethystinus* and unlike *S. tartari*, the micronuclei do not occur in macronuclear depressions, but unlike the report of Nilsson, a close association between micronuclei and pigment granules was not observed in our ultrastructural studies. We also note that, in contrast to Nilsson's written statement, the myonemal layer of the Australian isolate is perforated—although Nilsson's micrographs suggest that the myonemal layer in her isolates may have discontinuities. We regard the differences as minor, and regard our observations to be of the same species as those of Nilsson on the taxon referred to as *S. amethystinus*, and that this can be distinguished from *S. tartari* on nuclear morphology.

Stentor niger can be distinguished from *S. amethystinus* and the organisms observed by us because it lacks symbiotic algae (Foissner & Wölfl, 1994). Like *S. amethystinus* it has a single macronucleus and the cell tends to be conical in shape. Although generally larger than the cells observed by us, the size range of 250–300 µm does overlap with that reported for *S. amethystinus* (Table 1). As some ciliates with symbiotic algae may loose them, it is possible that *S. niger* is conspecific variety of *S. amethystinus*.

Stentor igneus has a single macronucleus, but with a length of about 100 µm, an ability to adopt the elongate body form, and the absence of symbiotic algae, it can be distinguished from *S. amethystinus* and the organisms observed by us. One isolate has, however, been reported with algae (Foissner & Wölfl, 1994).

Stentor fuliginosus was inadequately described as a variety of *S. igneus* from America, has only recently been given a clear identity (Foissner & Wölfl, 1994). It can be found as a short conical form or as an elongate form. It is relatively small—Foissner & Wölfl suggest that it is usually under 150 µm—but extended cells may be as long as 300 µm. These authors do reflect on possible synonymy with *S. amethystinus* but note that the micronuclei of *S. fuliginosus* are not surrounded by pigment granules. We note that *S. fuliginosus* has a smaller macronucleus and more adoral membranelles than the organisms observed by us. We do not therefore regard our observations to be of *S. fuliginosus sensu* Foissner & Wölfl.

Comparison is therefore best made with the species referred to as *S. amethystinus*. The original description of *S. amethystinus* was by Leidy and reported anonymously to the Academy of Natural Sciences of Philadephia (Anonymous, 1880). It is an incomplete account, lacks illustrations, but referred to a ciliate that measured up to 820 µm long and was encountered readily in an extended form. A number of workers have since referred to and added new observations about this species (Table 1). Of these, only Dragesco (1970) has made new observations on an isolate that adopts the extended trumpet shape. All other records are of an organism that only adopts a rounded or short conical form (Nilsson, 1986; Foissner *et al.*, 1992; Foissner & Wölfl, 1994; Schneider, 1991). The Australian isolate broadly agrees in shape, overlaps in size range, has similar macronuclei and micronuclei (where they have been recorded) with these records from Europe. The Australian isolates do not achieve the same maximum size, have more kineties, and differs subtly in myonemal organization and proximity of pigment granules to the micronuclei.

Dragesco's African isolate does not achieve the same maximal size as the American or European isolates. Sometimes it has more than one macronucleus (see Nilsson, 1986). It may occasionally lack symbiotic algae (see also comments to *S. niger* above). Dragesco & Dragesco-Kernéis (1986) comment that they do not think that the African isolate is the same species as the European isolate. The Australian isolates differ from the African isolate in being smaller, and not being capable of adopting the extended form.

It would appear then that there are subtle differences among different geographical isolates of *S. amethystinus* and these are of comparable magnitude as between *S. amethystinus* and some other brown species of *Stentor*. Because of differences in maximum size and the capacity to adopt a trumpet-shape, we do not believe that the isolates observed by Leidy are identical to those observed by Nilsson (1986), Foissner *et al.* (1992), Foissner & Wölfl (1994) and Schneider (1991), nor to those observed by Dragesco or by us. Indeed, we believe that Leidy's observations were of organisms which more closely correspond with *S. fuliginosus* because of its larger size and occurrence of an extended form. *Stentor fuliginosus* was originally reported from North America. If we were to regard *S. fuliginosus* to be a junior synonym of *S. amethystinus*, it would require that the European isolates be given a new name. Given the inadequacy of the original descriptions of both *S. amethystinus* and *S. fuliginosus* and given that we are unable to assess if the subtly different isolates represent incomplete documentation of a continuum of form or if they represent stable discontinuities (species), we believe that no benefits would accrue from this course of action, and there would be disadvantages of nomenclatural instability. Given that at least one clear

Table 1. Summary of reported characteristics of *Stentor amethystinus*. Dash = not specified; AZM = adoral zone of membranelles.

	Leidy in Anonymous 1880	Kahl, 1932	Tartar, 1961	Dragesco, 1970	Foissner, 1980	Nilsson, 1986	Schneider, 1992	Foissner *et al.*, 1992	Foissner & Wölfl, 1994	Australian isolate
Source	USA	—	—	Cameroon	Austria	Austria	Europe	—	—	Australia
Length (µm)	180–840 (long trumpet)	300–400	—	250–350	135–500	about 300	150–600	135–500	—	150–220
Kineties	—	—	—	90–100	60	80	—	90–110	90–120	80–100
Kineties in oral-region	—	—	—	—	25	—	—	20–25	20–25	28–32
Colour	lilac, amethystine	brown, amethystine	blue-violet	blue-violet	—	brownish	blue-violet, red-violet	dark-violet	violet to purple-red	dark plum, brownish
Shape	conical to extended	—	pyriform, conical	extended conical	spherical	short trumpet	conical	—	—	mostly conical
Extended form observed	yes	—	doesn't stretch	yes	no	no	no	—	—	no
Nucleus diameter (µm)	spherical, 30	—	oval	rounded, 23–30	rounded, 20–25	spherical	rounded, 25–30	rounded, 20–30	—	spherical-oval
Membranelles	—	—	—	160 in AZM	150	150	—	200–300 in AZM	200–300	190–200 in AZM
Zoochlorellae	(abundance of chlorophyll)	yes	yes	—	4–6 µm	4 µm	6 µm	4–7 µm	—	4 µm
Micronuclei	—	—	—	—	—	6 micronuclei close to macro-nucleus	—	—	—	at least 10 micro-nuclei, close to macronucleus

contemporary concept of *S. amethystinus* has emerged (Foissner & Wölfl, 1994) we believe that we will be better served by regarding the species observed by us as being the same as the European isolates and as *S. amethystinus*. We expect that future exploration of this taxon may lead to the concept of this species becoming broader to confidently include all geographic varieties and *S. fuliginosus*, or narrowed such that the geographical varieties are given specific status.

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Review of *Neoanchisquilla* Moosa, 1991 and *Neclorida* Manning, 1995 (Crustacea: Stomatopoda: Squilloidea), with Descriptions of Two New Species of *Neoanchisquilla* from the Indian Ocean

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ABSTRACT. *Neoanchisquilla* Moosa, 1991, is reviewed and two new species are described. *Neoanchisquilla tuberculata* and *N. australiensis* are described from the Comoro Islands and the Australian Northwest Shelf respectively, representing the first records of the genus from the Indian Ocean. The type species, *N. semblatae* Moosa, 1991, from New Caledonia, is redescribed. Both new species differ from *N. semblatae* in bearing seven teeth on the raptorial claw, and differ from each other in the dorsal and ventral ornamentation of the telson. A cladistic analysis supports the monophyly of *Neoanchisquilla* and shows the two newly described Indian Ocean species to be more closely related to each other than either is to the Western Pacific *N. semblatae*. Additional specimens of *Neclorida miersi* (Manning, 1968b) from Madagascar are the largest known specimens of the species, which is herein redescribed. Most diagnostic characters of the monotypic *Neclorida* are invariant with size, with the exception of the cornea width and the distinctness of the prelateral lobe of the telson. The generic diagnosis of *Neclorida* is emended to account for these new data.

AHYONG, SHANE T., 1998: Review of *Neoanchisquilla* Moosa, 1991 and *Neclorida* Manning, 1995 (Crustacea: Stomatopoda: Squilloidea), with descriptions of two new species of *Neoanchisquilla* from the Indian Ocean. *Records of the Australian Museum* 50(2): 217–229.

Examination of unidentified mantis shrimp (Stomatopoda) collections in the National Museum of Natural History, Smithsonian Institution, Washington D.C., revealed a specimen of an undescribed species of *Neoanchisquilla* Moosa, 1991, from the Comoro Islands, and additional specimens of a seldom reported species, *Neclorida miersi* (Manning, 1968b). A second species of *Neoanchisquilla* is described based on a single specimen from the Australian Northwest Shelf, in the collections of the Museum and Art Gallery of the Northern Territory.

Neoanchisquilla was established for *N. semblatae* Moosa, 1991, from New Caledonia. The two new species of *Neoanchisquilla*, are thus the first records of the genus from the Indian Ocean. The genus is herein reviewed based on re-examination of the holotype of *N. semblatae*. *Neoanchisquilla semblatae* is fully redescribed incorporating data not mentioned by Moosa (1991). Species of *Neoanchisquilla* resemble the monotypic *Anchisquilla* (Manning, 1968a), in almost every respect, sharing similar morphology and basic colour pattern. Although greatly similar, both genera were monotypic (sensu Manning, 1995) and obviously not problematic in terms of individual monophyly. The discovery of the two new species of *Neoanchisquilla*, however, prompted confirmation of their monophyly by cladistic analysis.

Neclorida Manning, 1995, is a monotypic genus erected for *Clorida miersi* Manning, 1968b. *Neclorida miersi* has been reported only from Indonesia and the type locality, Madagascar. The present specimens of *N. miersi* are the largest known to date, bearing characters requiring emendation to the generic diagnosis.

Materials and methods

Material for this study is deposited in the following institutions: Australian Museum (AM), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum and Art Gallery of the Northern Territory, Darwin (NTM), and National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM). Terminology and size descriptors generally follow the conventions of Manning (1969, 1978) supplemented by some abbreviations proposed by Makarov (1979). For brevity, the "basal prolongation of the uropod" (Manning, 1969) is herein referred to as the "uropodal protopod".

Abbreviations: abdominal somite (AS), antenna (A2), antennule (A1), cornea width (CW), intermediate (IM), lateral (LT), marginal (MG), maxilliped (MXP), median (MD), pleopod 1 (PLP1), submedian (SM), and thoracic somite (TS). All measurements are in millimetres (mm). Total length (TL) is measured along the midline from the tip of the rostrum to the apices of the submedian teeth. Carapace length (CL) is measured along the midline and excludes the rostral plate. Corneal index (CI) is given as 100CL/CW.

Phylogenetic analysis of *Neoanchisquilla* was based on 17 unordered morphological characters (Appendix 1, 2) using MacClade 3.04 (Maddison & Maddison, 1993) and the *exhaustive search* in PAUP 3.1.1 (Swofford, 1993). Uninformative characters (4, 9, 10, 12, 13, 15, 16) artificially "improve" the tree statistics, but were included to show the distribution of autapomorphies useful in species diagnoses. A separate analysis was also run excluding uninformative characters. To test the monophyly of *Neoanchisquilla* with respect to *Anchisquilla*, all species of both genera comprised the ingroup. Character states were polarized by outgroup comparison. Two species of the Indo-West Pacific genus, *Levisquilla, L. jurichi* (Makarov, 1979) and *L. minor* (Jurich, 1904) were selected as outgroups, based on their close relationship to *Anchisquilla* and *Neoanchisquilla* in preliminary phylogenetic analyses of the squilloid genera (in prep.). States corresponding to each character discussed in the text are given following the character number in brackets. For example, 4[1] means character 4, state 1.

Systematics

Squilloidea Latreille, 1803

Squillidae Latreille, 1803

Neoanchisquilla Moosa, 1991

Diagnosis. Eye with cornea bilobed; cornea broader than and set obliquely on stalk, width less than 1/3CL. Ophthalmic somite with rounded anterior margin. A1 somite not extending anteriorly beyond rostral plate. Carapace anterolateral angles armed; MD and IM carinae absent; LT carina indistinct, indicated posteriorly only; with indistinct reflected MG carina. Raptorial claw dactylus with more than 6 teeth; carpus dorsal carina undivided; merus outer inferodistal angle unarmed. Mandibular palp 3-segmented. MXP1–4 each with epipod. TS5–7 lateral processes single. TS5–8 and AS1–5 each lacking SM carinae. Telson SM teeth with movable apices; prelateral lobe present; dorsolateral surface with numerous supplementary longitudinal carinae or rows of tubercles. Uropodal protopod inner margin armed with slender spines.

Description. Total length of adults less than 100 mm. Dorsal integument smooth. Eye with cornea bilobed; cornea broader than and set obliquely on stalk, width less than 1/3CL. Ophthalmic somite with rounded anterior margin. Ocular scales broad, subtruncate, rounded laterally; separate. A1 somite not extending anteriorly beyond rostral plate; dorsal processes produced to a slender spine, apices directed anterolaterally. A2 scale slender; entire margin setose. Rostral plate lacking dorsal carinae. Carapace anterolateral angles armed; lacking dorsal carinae except for indistinct LT and reflected MG carinae indicated posteriorly; lacking posterior median projection. Raptorial claw dactylus with more than 6 teeth, outer margin broadly curved; proximal margin with distinct basal notch and blunt lobe proximally; carpus dorsal carina undivided; merus outer inferodistal angle unarmed; propodus opposable margin pectinate, with 3 movable spines proximally, distal margin lacking stout tooth; merus outer inferodistal angle unarmed; basis lacking ventrally directed mesial spine. Mandibular palp 3-segmented. MXP1–4 each with epipod. MXP5 basal segment lacking ventrally directed spine. Pereiopods 1–3 basal segment unarmed; endopod segments fused, slender, entire margin setose. TS6–8 each with IM carinae, lacking SM carinae. TS5 lateral process a single, short spine, directed anterolaterally, inclined ventrally; ventral spine slender, directed ventrally. TS6–7 lateral processes single. TS8 anterolateral margin

obtusely rounded. AS1–5 each lacking SM carinae; with distinct IM, LT and MG carinae. AS6 with SM, IM and LT carinae; sternum posterior margin unarmed. Telson broader than long, flattened, trianguloid, with 3 pairs of primary marginal teeth (SM, IM, LT), each with dorsal carina; SM teeth with minute movable apices; prelateral lobe present; SM, IM and LT denticles spiniform, lacking dorsal tubercle; MD carina low, interrupted proximally, armed posteriorly with apical spine overhanging blunt tubercle; dorsolateral surface with numerous supplementary longitudinal carinae or tubercles. Telson ventral surface with long postanal carina; ventrolateral carina extending posteriorly to base of lateral tooth. Uropodal protopod terminating in 2 slender spines, inner longer; dorsally and ventrally carinate; unarmed dorsally excepting dorsal spine above proximal exopod articulation; protopod inner margin armed with slender spines; with rounded, flattened ventral lobe anterior to endopod articulation. Uropodal exopod proximal segment unarmed dorsally; exopod distal segment ovate, elongate. Uropodal exopod proximal segment with inner margin lacking prominent, rounded distal lobe; outer margin with graded movable spines; distal margin with slender ventral spine. Uropodal exopod proximal segment unarmed dorsally; endopod unarmed dorsally, entire margin setose.

Included species. *Neoanchisquilla australiensis* n.sp., *N. semblatae* Moosa, 1991 and *N. tuberculata* n.sp.

Remarks. Both cladistic analyses, including and excluding uninformative characters, found a single, identical tree (Fig. 1) supporting monophyly of *Neoanchisquilla*. The only synapomorphy of *Neoanchisquilla* identified here is the rounded anterior margin of the ophthalmic somite (1[1]). *Neoanchisquilla*, however, also differs from *Anchisquilla* in bearing indistinct lateral carinae on the carapace, there are more than six teeth on the dactylus of the raptorial claw, the proximal margin of the dactylus is distinctly notched and the SM teeth of the telson bear movable apices. Most of these characters distinguishing *Neoanchisquilla* from *Anchisquilla* are plesiomorphies (4[1], 9[0], 12[0]).

Phylogenetic relationships within *Neoanchisquilla* correlate with known geographical distributions. Hence, the two Indian Ocean species, *N. australiensis* and *N. tuberculata*, are more closely related to each other than either is to *N. semblatae* from the western Pacific. In contrast, *Anchisquilla fasciata*, occurs throughout the Indo-West Pacific (Manning, 1995). Future sampling, nevertheless, may show vastly different distribution patterns for species of *Neoanchisquilla* which are presently known only from type material.

Key to species of *Anchisquilla* and *Neoanchisquilla*

1 Dactylus of raptorial claw with 6 teeth. SM teeth of the telson with fixed apices. Ophthalmic somite anterior margin triangular ..... *Anchisquilla fasciata*

—— Dactylus of raptorial claw with more than 6 teeth. SM teeth of the telson with movable apices. Ophthalmic somite anterior margin rounded 2

2 Rostral plate ovoid; apex broadly rounded. Carapace anterolateral spines extending to base of rostral plate. Dactylus of raptorial claw with 8 teeth. Telson dorsal surface lacking accessory median carina ..... *Neoanchisquilla semblatae*

—— Rostral plate triangular; apex narrow, blunt. Carapace anterolateral spines small, not extending to base of rostral plate. Dactylus of raptorial claw with 7 teeth 3

3 Telson with numerous curved rows of tubercles. TS6–7 lateral processes flattened, margin slightly sinuous. Ventral surface of telson with rows of tubercles adjacent to postanal carina ..... *Neoanchisquilla tuberculata* n.sp.

—— Telson with numerous undivided carinae. TS6–7 lateral processes broadly rounded. Ventral surface of telson lacking rows of tubercles adjacent to postanal carina ..... *Neoanchisquilla australiensis* n.sp.

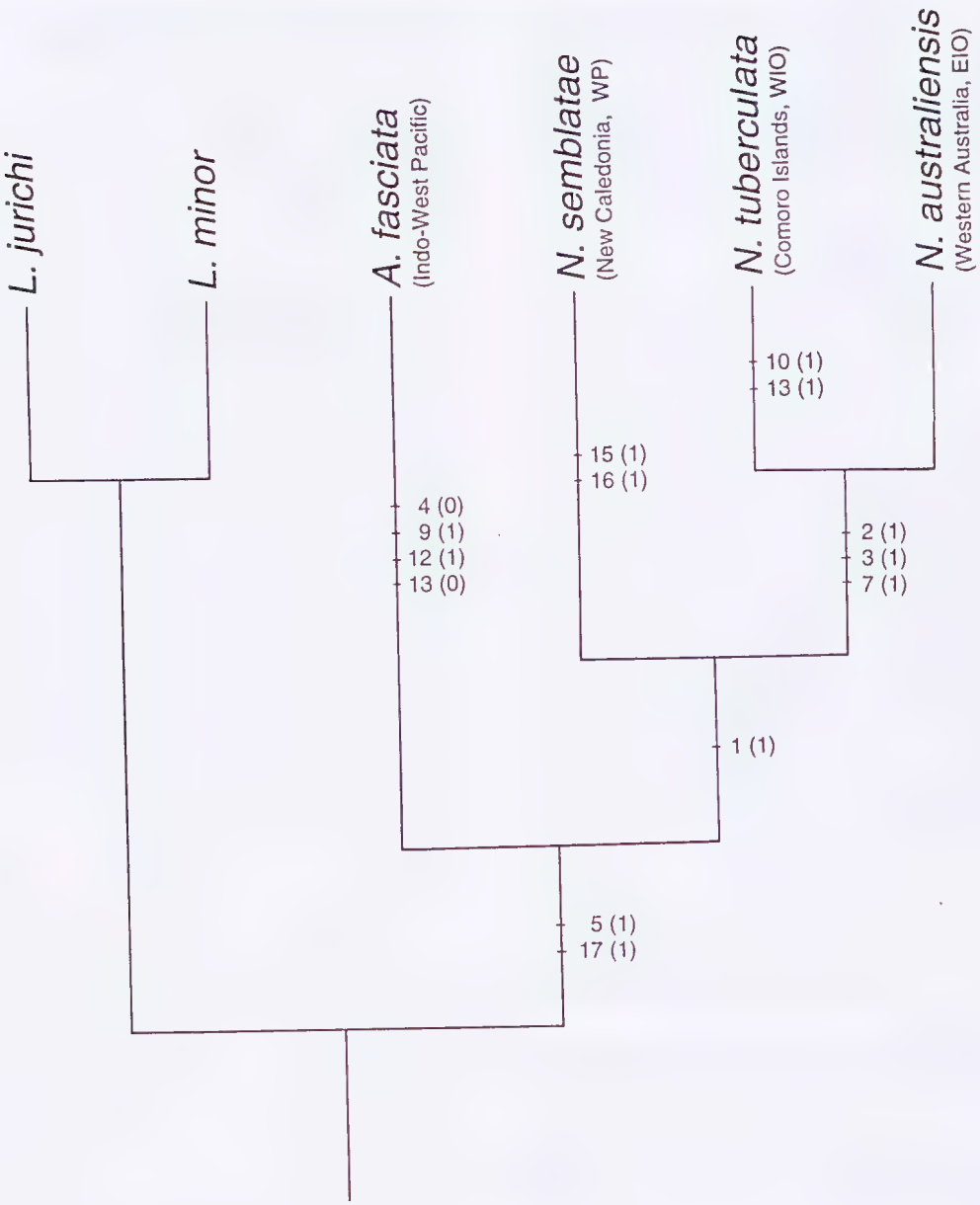

Figure 1. Single most parsimonious cladogram of *Neoanchisquilla* using all 17 characters (length 23, ci 0.87, hi 0.13, ri 0.75). Excluding uninformative characters produced an identical tree of length 15 steps, ci 0.80, hi 0.20 and ri 0.75. EIO, Eastern Indian Ocean; IWP, Indo-West Pacific; WIO, Western Indian Ocean; WP, Western Pacific. Outgroups: *Levisquilla minor, L. jurichi*. Ingroup: *Anchisquilla fasciata, N. australiensis, N. semblatae, N. tuberculata*. Apomorphic characters and states (parentheses) are indicated on each branch of the ingroup.

Neoanchisquilla australiensis n.sp.

Fig. 2

Type material. HOLOTYPE: NTM Cr012355, female (TL 25 mm), Northwest Shelf, Western Australia, 19°58.6–59.1'S 117°49.0–49.4'E, 43 m, beam trawl, FRV Soela, 25 June 1983.

Diagnosis. Rostral plate slightly longer than broad; triangular; apex narrow, blunt. Raptorial claw dactylus with 7 teeth. TS6–7 lateral processes broadly rounded. Abdominal carinae spined as follows: SM 6, IM 6, LT 6, MG 2–5. Telson dorsal surface with median carina and numerous undivided carinae; ventral surface lacking rows of tubercles lateral to postanal carina.

Description of holotype. TL 25 mm. Eye small; stalk moderately inflated; cornea bilobed, extending slightly beyond A1 peduncle segment 1; CI 421. A1 peduncle 0.85CL. A1 somite dorsal processes with acute apices. Antennal scale length 0.48CL. Rostral plate slightly longer than broad; triangular; apex rounded. Carapace anterior width 0.50CL; anterolateral spines small, not extending

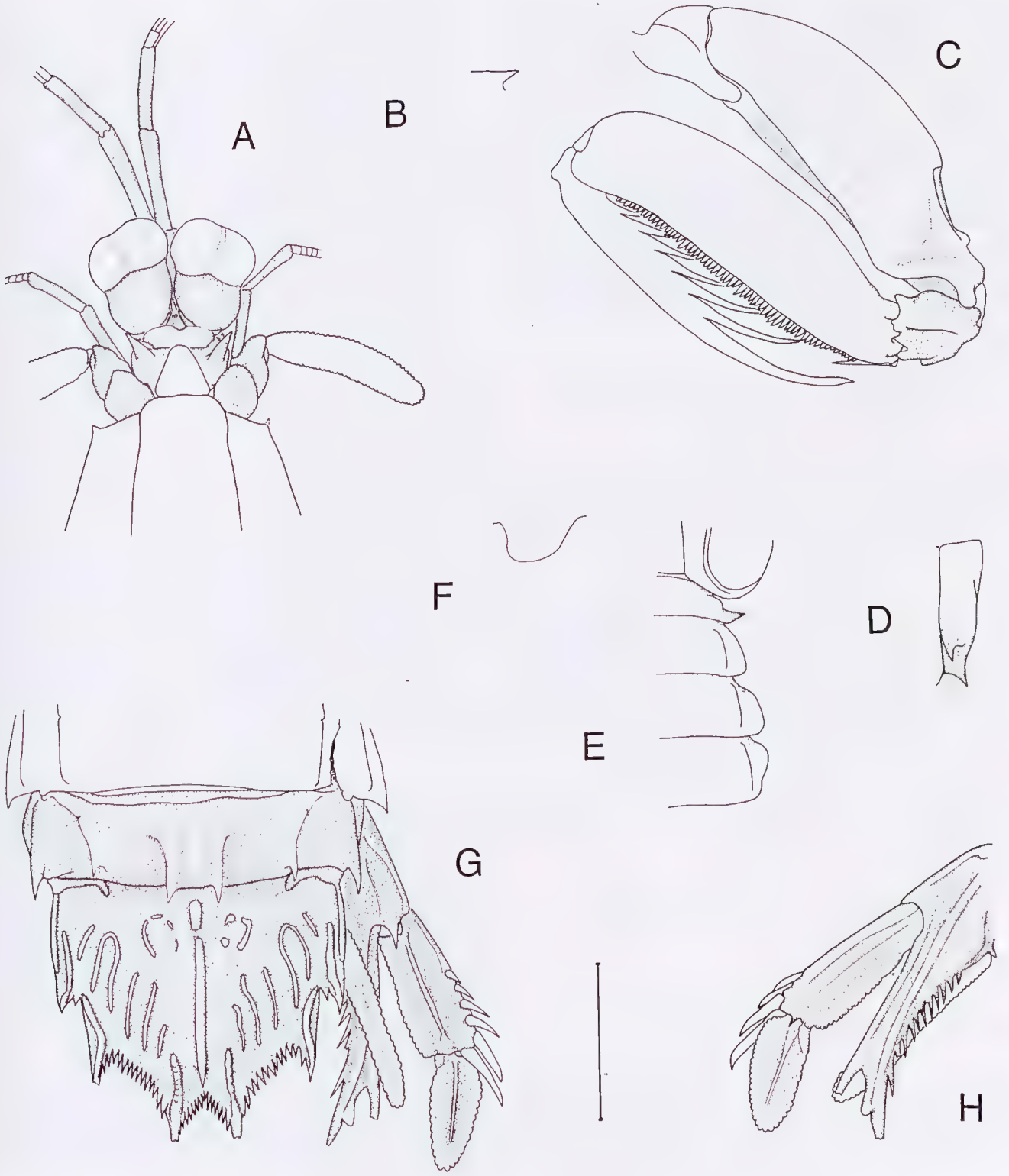

Figure 2. *Neoanchisquilla australiensis* n.sp. holotype. A, anterior cephalon, dorsal; B, A1 somite dorsal process, right lateral; C, raptorial claw, right lateral; D, TS5, right lateral; E, posterior carapace and TS5–8 lateral processes, right dorsal; F, TS8 sternal keel, right lateral; G, AS5–6, telson and uropod, dorsal; H, uropod, right ventral. Scale bar: A–E, G, 2.5 mm; F, 1.2 mm.

to base of rostral plate. Raptorial claw dactylus with 7 teeth. TS6–7 lateral processes broadly rounded. TS8 sternal keel subtruncate. AS6 with blunt tubercle anterior to uropodal articulation. Abdominal carinae spined as follows: SM 6, IM 6, LT 6, MG 2–5. Telson prelateral lobe faintly indicated, longer than margin of lateral tooth; denticles 7, 12–14, 1. Dorsolateral surface lacking accessory median carina; with six, well-developed supplementary longitudinal carinae; proximally with short, irregular carina and tubercles adjacent to median carina. Carinae of primary

teeth sinuous, irregular. Telson ventral surface with long, smooth postanal carina, lacking carinae or tubercles laterally, extending about 0.8 distance between anal pore and posterior margin. Uropodal protopod inner margin armed with 11 slender spines; with rounded, flattened ventral lobe anterior to endopod articulation. Terminal spines of uropodal protopod with lobe on outer margin of inner spine rounded, broader than adjacent spine, proximal margin concave. Uropodal exopod proximal segment with 6 graded movable spines on outer margin, distal 2 flattened with acute apices, distalmost slightly exceeding midlength of distal segment. Exopod distal segment shorter than proximal segment. Uropodal exopod proximal segment lacking tubercles ventrally, adjacent to articulation with protopod.

Measurements. Holotype female: TL 25 mm, CL 5.9 mm, CW 1.4 mm, A1 peduncle length 5.0 mm.

Colour in alcohol. Almost completely faded. Dark pigmentation around reflected marginal carina of the carapace; occasional scattered chromatophores laterally. A2 scale with black apex.

Remarks. The similarities and differences between *N. australiensis* and *N. tuberculata* are outlined under the account of the latter. *Neoanchisquilla australiensis* differs from *N. semblatae* in bearing seven instead of eight teeth on the dactylus of the raptorial claw; the rostral plate is triangular with a blunt, narrow apex, fewer intermediate carinae on the abdominal somites are armed, and the prelateral lobe of the telson is relatively longer.

Distribution. Known only from the type locality, the Australian Northwest Shelf.

Neoanchisquilla semblatae Moosa, 1991

Fig. 3

Neoanchisquilla semblatae Moosa, 1991: 208–210, fig. 15.–Richer de Forges & Moosa, 1992: 152.–Manning, 1995: 25.

Material. HOLOTYPE: MNHN Sto 1626, male (TL 26 mm), Chesterfield Islands, New Caledonia, 20°34.37'S 160°51.80'E, 74 m, CORAIL 2 stn DW 30, mud and calcareous sediment with *Halimeda*, July to August 1988.

Diagnosis. Rostral plate with broadly rounded apex. Raptorial claw dactylus with 8 teeth. TS6–7 lateral processes flattened, margin slightly sinuous. Abdominal carinae spined as follows: SM 6, IM 6, LT 4–6, MG 1–5. Telson dorsal surface with median carina and numerous undivided curved carinae, lacking accessory median carina; ventral surface lacking rows of tubercles either side of postanal carina.

Description of holotype. TL 26 mm. Eye small; stalk moderately inflated; cornea bilobed, extending slightly beyond A1 peduncle segment 1; CI 446. A1 peduncle 0.97CL. A1 dorsal processes slender, apices blunt, directed anterolaterally. A2 scale length 0.53CL. Rostral plate ovoid; slightly longer than broad; apex broadly rounded. Carapace anterior width 0.51CL; carapace anterolateral spines slender, extending to base of rostral plate. Raptorial claw dactylus with 8 teeth. TS6–7 lateral processes flattened, margin slightly sinuous. TS8 sternal keel rounded. AS6 with ventrolateral spine anterior to uropodal articulation. Abdominal carinae spined as follows: SM 6, IM 6, LT 4–6, MG 1–5 (AS2 unarmed on left side). PLP1 endopod in male with slender, curved hook process and broad, flattened tube process; apex of hook process blunt, exceeding apex of distal endite. Telson prelateral lobe length subequal to or slightly longer than margin of lateral tooth; denticles 7, 12–13, 1. Dorsolateral surface lacking accessory median carina; with 5–6 supplementary longitudinal carinae, several sinuous proximally. Carinae of primary teeth sinuous, irregular. Telson ventral surface with long, smooth postanal carina, lacking carinae or tubercles laterally, extending about 0.8 distance between anal pore and posterior margin. Uropodal protopod inner margin armed with 10–12 slender spines. Terminal spines of uropodal protopod with lobe on outer margin of inner spine rounded, broader than adjacent spine, proximal margin concave. Uropodal exopod proximal segment with 6 graded movable spines on outer margin, distal 2 flattened with acute apices, distalmost slightly exceeding midlength of distal segment. Exopod distal segment with length subequal to proximal segment. Uropodal endopod lacking tubercles ventrally, adjacent to articulation with protopod.

Colour in alcohol. A1 and A2 peduncles pale. A2 scale with dark posterior margin and apex. Carapace with dark anterior margin and four, broad, diffuse, irregular transverse bands; reflected marginal carinae enclosing black patch with diffuse margins. Thoracic and abdominal somites each with broad, diffuse submedian patches, with darker distal patch between intermediate and lateral carinae extending onto following somite. Telson with broad, diffuse, dark patch covering intermediate and lateral teeth; with broad, diffuse longitudinal median band extending from anterior margin to apices of SM teeth, excepting a short, unpigmented area distally. Raptorial claw, maxillipeds, pereiopods and pleopods unpigmented. Uropodal protopod inner margin and endopod dark; exopod proximal segment dark on outer distal half and articulation with distal segment; exopod distal segment with diffuse pigmentation on proximal and outer margin.

Measurements. Holotype male: TL 26 mm, CL 5.8 mm, CW 1.3 mm, A1 peduncle length 5.6 mm.

Remarks. In *N. semblatae* the apically rounded hook process of the male PLP1 endopod (15[1]) is unusual, because it is produced to a sharp point in *N. tuberculata*, *A. fasciata* and other *Clorida*-like genera such as *Cloridina*, *Neclorida*, *Lenisquilla* and *Levisquilla*. The condition of the hook-process in *N. semblatae* is unlikely to be size related because the penes are well developed,

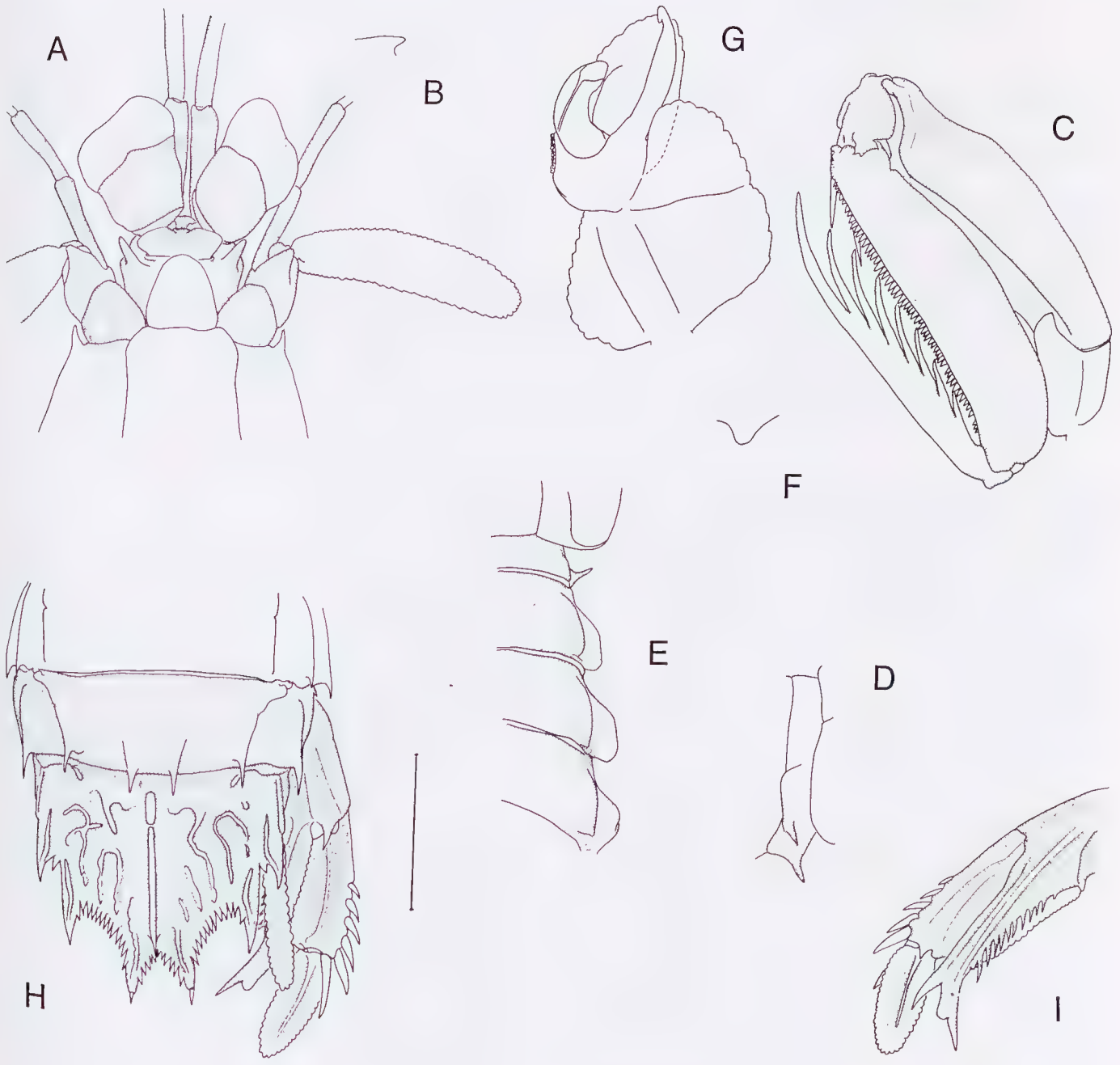

Figure 3. *Neoanchisquilla semblatae* Moosa, 1991. holotype. A, anterior cephalon, dorsal; B, A1 somite dorsal process, right lateral; C, raptorial claw, left lateral; D, TS5, right lateral; E, posterior carapace and TS5–8 lateral processes, right dorsal; F, TS8 sternal keel, right lateral; G, PLP1 endopod; H, AS5–6, telson and uropod, dorsal; I, uropod, right ventral. Scale bar A–B, D–F, 2 mm; C, H, I, 3 mm; G, 1 mm.

the male PLP1 endopod is fully formed and the sharp apex of the hook process is well developed even in juveniles of *A. fasciata* and species of other *Clorida*-like genera. The hook process in *N. semblatae* is also distinctly longer than in *N. tuberculata* n.sp., exceeding the distal margin of the distal endite (16[1]). Male PLP1 characters should readily distinguish *N. semblatae* from *N. tuberculata*, but unfortunately the male PLP1 of *N. australiensis* is unknown.

Richer de Forges & Moosa (1992) noted that the habitats around the Chesterfield Islands, the type locality of *N. semblatae*, are principally coralline, with fine sediments and carbonated mud. Collection data in Moosa (1991) show that no other stomatopods were collected from the same station as *N. semblatae*.

Distribution. Known only from the type locality, Chesterfield Islands, New Caledonia.

Neoanchisquilla tuberculata n.sp.

Fig. 4

Material. HOLOTYPE: USNM 260879, male (TL 74 mm), Comores, 12°11'09"S 44°19'03"E, 9–20 m, RW88–26, coll. R. Winterbottom, 21 November 1988.

Diagnosis. Rostral plate triangular; longer than broad; apex narrow, blunt. Carapace anterolateral spines small, not extending to base of rostral plate. Raptorial claw dactylus with 7 teeth. TS6–7 lateral processes flattened, margin slightly sinuous. Abdominal carinae spined as follows: SM 6, IM 6, LT 2–6, MG 1–5; sternum posterior margin unarmed. Telson dorsal surface with MD carina, tuberculate accessory MD carina and numerous curved rows of tubercles; ventral surface with 2 rows of irregularly spaced tubercles lateral to postanal carina.

Description of holotype. TL 74 mm. Eye with cornea strongly bilobed, not extending beyond A1 peduncle segment 1; CI 480. A1 peduncle 0.86CL. A1 dorsal processes with spiniform apices, directed anterolaterally. A2 scale length 0.62CL. Rostral plate triangular; slightly longer than broad; apex blunt. Carapace anterior width 0.55CL; anterolateral spines small, not extending to base of rostral plate. Raptorial claw dactylus with 7 teeth. TS6–7 lateral processes flattened, margin slightly sinuous. TS8 sternal keel subtruncate. AS6 with minute ventrolateral spine anterior to uropodal articulation. Abdominal carinae spined as follows: SM 6, IM 6, LT 2–6, MG 1–5; sternum posterior margin unarmed. PLP1 endopod in male with slender, curved hook process and broad, flattened tube process; apex of hook process acute, exceeding apex of tube process. Telson prelateral lobe longer than margin of LT tooth; denticles 7–8, 17–18, 1. Dorsolateral surface with proximal cluster of tubercles, tuberculate accessory MD, and 7–8 curved rows of closely set tubercles. Carinae of primary teeth tuberculate. Telson ventral surface with tuberculate postanal carina and 2 rows of irregularly spaced tubercles laterally. Uropodal protopod inner margin armed with 15–18 slender spines. Terminal spines of uropodal protopod with lobe on outer margin of inner spine rounded to angular, narrower than adjacent spine, proximal margin concave. Uropodal exopod proximal segment with 7 graded movable spines on outer margin, distal 2 flattened with acute apices, distalmost not exceeding midlength of distal segment. Exopod distal segment with length subequal to proximal segment. Uropodal endopod with row of 3 tubercles ventrally, adjacent to articulation with protopod.

Colour in alcohol. Rostral plate, antennal protopods and anterior cephalon dark brown. A1 and A2 peduncles pale. A2 scale with dark posterior margin and apex. Carapace with dark anterior margin and three, broad, diffuse, irregular transverse bands; reflected marginal carinae enclosing black patch with diffuse margins. Thoracic and abdominal somites each with posterior margin dark; broad, diffuse submedian patches, with darker distal patch between intermediate and lateral carinae extending onto following somite. Telson with darkly pigmented carinae; with broad, diffuse, dark patch covering intermediate and lateral teeth; with broad, diffuse longitudinal median band extending from anterior margin to apices of SM teeth, excepting a short, unpigmented rectangle distally. Raptorial claw propodus with dark opposable margin and dark articulation with carpus; carpus dark; merus dark distally, ventrally and dorsally, unpigmented midlaterally; meral depression unpigmented excepting black trapezoid spot proximally. Pereiopods with dark protopod. Uropodal protopod and endopod dark; exopod proximal segment dark on distal half and articulation with distal segment; exopod distal segment dark along midline and outer margin.

Measurements. Holotype male: TL 74 mm, CL 16.8 mm, CW 3.5 mm, A1 peduncle 14.5 mm.

Etymology. Named for the tuberculate dorsal ornamentation of the telson.

Remarks. *Neoanchisquilla tuberculata* is unique in the genus in bearing tuberculate dorsal and ventral telson ornamentation (10[1], 13[1]). *Neoanchisquilla tuberculata* n.sp. also differs from *N. semblatae* in bearing fewer teeth on the raptorial claw (seven instead of eight); in having shorter anterolateral spines of the carapace; in having a narrower, more pointed apex of the rostral plate; the hook process of the male PLP1 endopod is shorter and apically acute; more lateral carinae on the abdominal somites are armed; the cornea is distinctly bilobed; the inner margin of the uropodal protopod bears 15–18 instead of 10–12 spines; and there are more movable spines on the outer margin of the uropodal exopod. Although an adult (Moosa, 1991), the holotype of *N. semblatae* is small (TL 26 mm). The first four distinguishing characters are unlikely to change with age but the latter four may be size related and should be used with caution.

Neoanchisquilla tuberculata is most closely related to *N. australiensis* in sharing a similar rostral plate, short anterolateral spines of the carapace, and seven teeth on the dactylus of the raptorial claw (2[1], 3[1], 7[1]). As well as the tuberculate dorsal and ventral telson ornamentation, *N. tuberculata* differs from *N. australiensis* in the shape of the cornea, in bearing truncate lateral processes of TS6–7, in having more abdominal somites with armed lateral carinae and in having a tuberculate accessory median carinae. Whereas the dorsolateral carinae of the telson are sharp and well formed in *N. australiensis*, the accessory median carina is completely suppressed.

Other than *N. semblatae* and *N. australiensis*, the only other species likely to be confused with *N. tuberculata* is *Anchisquilla fasciata* (De Haan). Ghosh (1973) reported material of *A. fasciata* from the Gulf of Oman which differed from the account of Kemp (1913) in bearing interrupted, instead of entire, dorsal carinae and

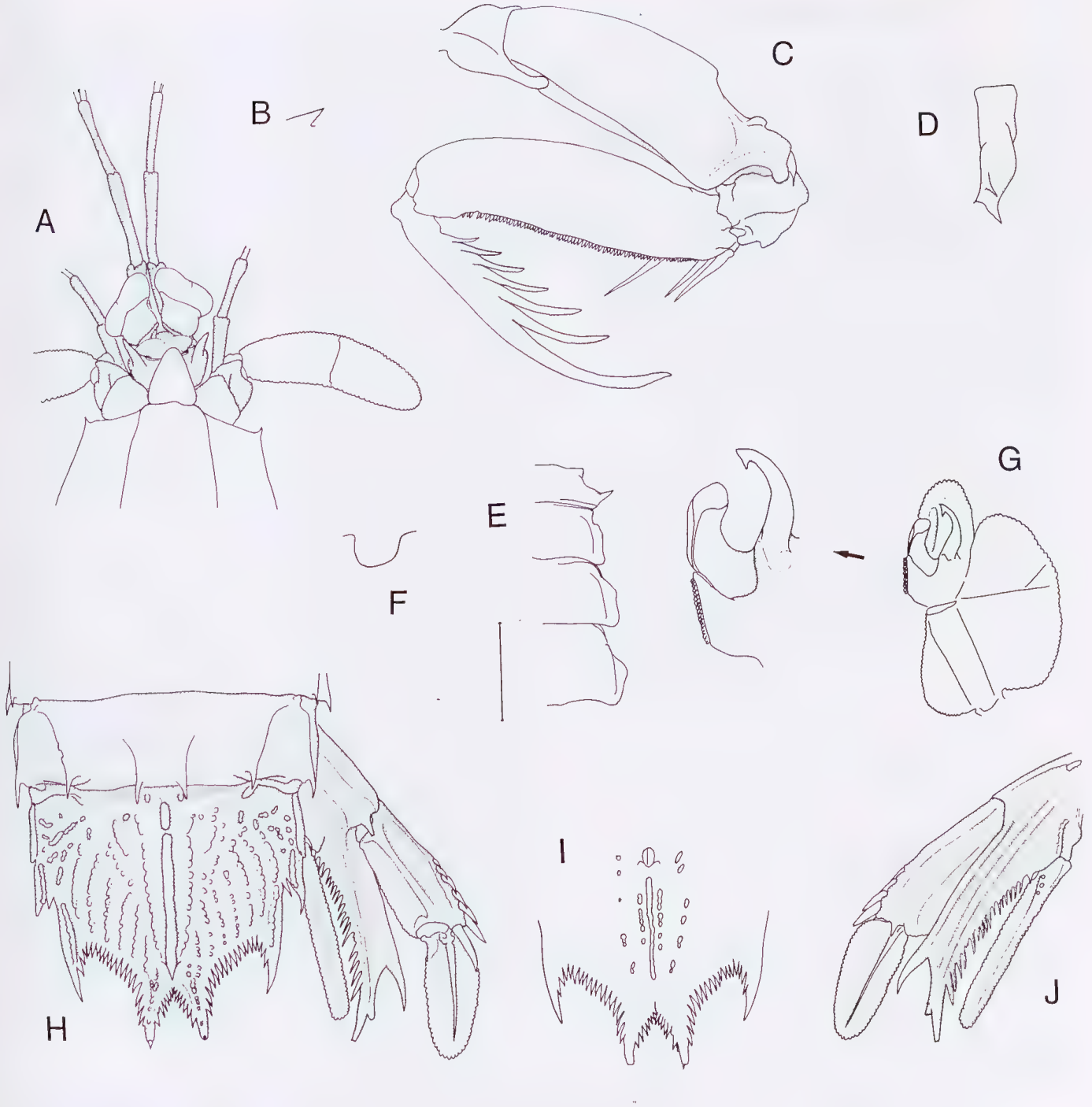

Figure 4. *Neoanchisquilla tuberculata* n.sp. holotype. A, anterior cephalon, dorsal; B, A1 somite dorsal process, right lateral; C, raptorial claw, right lateral; D, TS5, right lateral; E, TS5–8 lateral processes, right dorsal; F, TS8 sternal keel, right lateral; G, PLP1 endopod; H, AS5–6, telson and uropod, dorsal; I, telson, ventral; J, uropod, right ventral. Scale bar A–E, H–J, 5 mm; F, 3.5 mm; G, 2.4 mm.

lacking supplementary ventral carinae on the telson. Although *A. fasciata* may lack supplementary ventral carinae on the telson, the dorsal carinae are entire or only interrupted proximally. Ghosh (1973) may have been dealing with *N. tuberculata*, but his account is unfortunately too brief to confirm the identity of his material.

Distribution. Known from the type locality, the Comoro Islands, and possibly the Gulf of Oman.

Neclorida Manning, 1995

Diagnosis. Eye with cornea distinctly bilobed, broader than and set transversely on stalk; stalk slightly inflated. Ocular scales fused, faintly emarginate medially. A1 somite not extending anteriorly beyond rostral plate. Carapace with anterolateral spines; lacking carinae excepting reflected marginal carinae. Raptorial claw dactylus with 5 teeth. Mandibular palp present. MXP1–4 each with epipod. TS5–8 each lacking SM carinae. TS5–7 lateral processes single. AS1–4 each lacking SM carinae. Telson inflated; SM teeth with movable apices; prelateral lobe present (indistinct in juveniles and subadults); dorsolateral surface with numerous longitudinal rows of blunt tubercles; ventral surface with postanal and ventrolateral carina only. Uropodal protopod terminating in 2 slender spines; inner margin armed with numerous slender spines.

Included species. *Neclorida miersi* (Manning, 1968b).

Remarks. As noted by Manning (1968b, 1995), *Neclorida miersi* most closely resembles species of *Clorida* and *Cloridina*, in particular, *Cloridina verrucosa* (Hansen, 1926). The key feature distinguishing *Neclorida* from *Clorida* and *Cloridina* is the strongly bilobed cornea, which may be prove to be an autapomorphy. The monophyly of *Clorida* and *Cloridina* with respect to *Neclorida* remains to be tested.

Neclorida miersi (Manning, 1968b)

Fig. 5

Clorida miersi Manning, 1968b: 11–14, fig. 3.–Moosa, 1973: 22.–Moosa & Cleva, 1984: 77.
Neclorida miersi.–Manning, 1995: 25, 219.

Material. HOLOTYPE: USNM 124091, male (TL 33 mm), western coast of Madagascar, Banc de Pracel, 65 m, sand, coll. A. Crosnier, June 1959. USNM 124091, 1 male (TL 84 mm), 1 female (TL 85 mm), Entre Majunga et baie de Narendry, northwestern Madagascar, 40 m, coll. R. Plante, 14–15 April 1970.

Description. TL of adults to 85 mm. Dorsal integument smooth, polished. Eye with cornea distinctly bilobed, broader than and set transversely on stalk not extending beyond A1 peduncle segment 1; stalk slightly inflated; CI 400–683. Ocular scales fused, faintly emarginate anteriorly. Ophthalmic somite with triangular anterior margin. A1 peduncle 0.67–0.74CL. A1 somite dorsal processes slender, with spiniform apices, directed anterolaterally. A2 scale length 0.41–0.42CL. Rostral plate longer than broad; lateral margins convergent; apex rounded; lacking dorsal carinae. Carapace anterior width 0.41–0.45CL; anterolateral spines not extending to base of rostral plate; with reflected MG carinae only; lacking posterior median projection. Raptorial claw dactylus with 5 teeth, outer margin broadly curved, proximal margin with basal notch; carpus dorsal carina undivided; propodus opposable margin sinuous; merus outer inferodistal angle unarmed; basis lacking ventrally directed mesial spine. Mandibular palp 3-segmented. MXP1–4 each with epipod. MXP5 basal segment lacking ventrally directed spine. Pereiopods 1–3 basal segment unarmed; endopod 2-segmented, slender, entire margin setose. TS5–8 each lacking SM carinae. TS5 lateral process a single, short spine, directed anterolaterally and inclined ventrally; ventral spine triangular, acute, directed ventrally. TS6–7 lateral processes rounded to obtuse anterolaterally and posterolaterally. TS8 anterolateral margin triangular; sternal keel rounded. AS1–4 each lacking SM carinae. AS5 at most with faint indication of SM carina. AS6 with surface between SM and IM carinae irregularly sculptured; with ventrolateral spine anterior to uropodal articulation; sternum posterior margin unarmed. Abdominal carinae spined as follows: SM 6, IM 4–6 (5–6), LT 5–6, MG (3–4)5. Telson inflated, broader than long; SM teeth with movable apices; prelateral lobe shorter than margin of lateral tooth; median carina low, uninterrupted proximally, armed posteriorly; dorsolateral surface with accessory median carina composed of 4–5 tubercles and with numerous longitudinal rows of blunt tubercles; denticles triangular, 2–3, 7–8, 1; carinae of marginal teeth inflated in adult males. Telson ventral surface with long, tuberculate postanal carina; ventrolateral carina short, extending distally slightly beyond prelateral lobe. Uropodal protopod terminating in 2 slender spines, inner longer, dorsally and ventrally carinate; unarmed dorsally excepting dorsal spine above proximal exopod articulation; outer margin smooth; inner margin armed with 7–10 slender spines; with short ventral spine anterior to endopod articulation. Terminal spines of uropodal protopod with lobe on outer margin of inner spine rounded, deflected dorsally, broader than adjacent spine, proximal margin concave. Uropodal exopod proximal segment with broad, round distal lobe on inner distal half; outer margin with 6–7, graded movable spines, distal 2 flattened with acute apices, distalmost not exceeding midlength of distal segment; distal margin with short ventral spine; inner distal portion dark. Uropodal exopod distal segment longer than proximal segment; dark on inner half only; endopod unarmed dorsally, entire margin setose.

Remarks. *Neclorida miersi*, as *Clorida miersi*, has been reported only from the type locality, Madagascar, (Manning, 1968b) and Indonesia (Moosa, 1973; Moosa & Cleva, 1984) from specimens of TL 55 mm or less. The present specimens are the largest known, but agree in most respects with the holotype and Indonesian specimens. The present specimens differ from the holotype in that the cornea is distinctly broader than the stalk (approximately 0.8 eye length) and more strongly bilobed than figured for the holotype (Manning, 1968b: fig. 3b); the ventral tubercle below the lateral process of TS5 is more distinct and acute; the intermediate carinae of AS4 and lateral carina of AS5 are armed posteriorly; the dorsal surface of AS6 between the SM and intermediate carinae is irregularly sculptured; the outer margin of the proximal segment of the exopod bears seven instead of six movable spines;

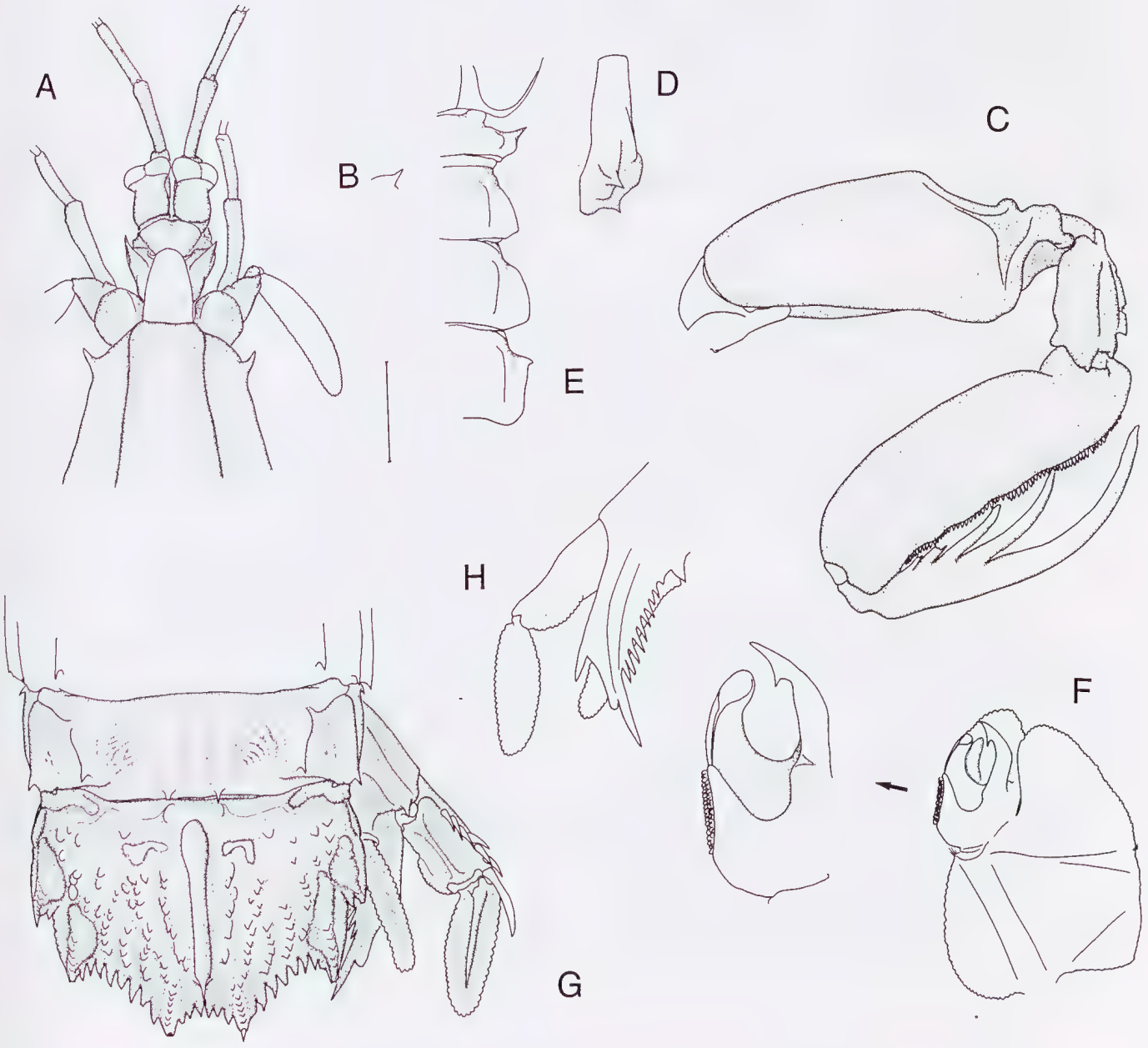

Figure 5. *Neclorida miersi* (Manning, 1968b) male (TL 84 mm), USNM 124091. A, anterior cephalon, dorsal; B, A1 somite dorsal process, right lateral; C, raptorial claw, right lateral; D, TS5, right lateral; E, posterior carapace and TS5–8 lateral processes, right dorsal; F, PLP1 endopod; G, AS5–6, telson and uropod, dorsal; H, uropod, right ventral. Scale bar A–E, G, H, 5 mm; F, 2.4 mm.

the inner margin of the uropodal protopod bears 7–10 spines instead of seven only; and the prelateral lobe of the telson is distinct. The large male differs from the large female and the holotype in bearing a slightly broader rostral plate, the PLP1 endopod is relatively larger than in the holotype, the marginal carinae of AS3–4 are armed and the dorsal ornamentation of the telson is inflated. All of the above differences are likely referable to size/age. Abdominal spination in the two largest specimens agrees with the 55 mm female reported by Moosa & Cleva (1984).

The dorsal ornamentation of the telson in the two largest specimens, the female in particular, closely resembles that of the holotype. The large male shows the inflated telson carinae and tubercles typical of adult males of similar genera such as *Clorida, Cloridina* and *Lenisquilla*. The most significant differences between the holotype and the largest specimens are in the cornea breadth (discussed above) and prelateral lobe on the telson. The prelateral lobe on the telson is an important diagnostic character for many genera and species. In the holotype of *Clorida miersi* the prelateral lobe is indistinct and considered absent in

the original diagnosis of *Neclorida*. *Neclorida miersi* therefore resembles species of *Clorida, Cloridina, Lenisquilla* and *Levisquilla*, in which the distinctness of the prelateral lobe increases with age/size, and this fact must be considered when identifying juveniles and subadults. The generic diagnosis of *Neclorida* is emended above to account for these new data.

Distribution. Known only from Madagascar and Indonesia in depths between 40 and 65 m.

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Appendix 1. Characters and states used in phylogenetic analysis of *Neoanchisquilla*.

1 Ophthalmic somite anterior margin: triangular (0); rounded (1).
2 Rostral plate: apex broad (0); apex narrow (1).
3 Carapace anterolateral spines: long, slender (0); short, triangular (1).
4 Lateral carina of carapace: distinct (0); indistinct (1).
5 Mandibular palp: absent (0); present (1).
6 TS6–7 lateral process: rounded (0); sinuous or flattened (1).
7 TS8 sternal keel: apex narrow (0); apex broad (1).
8 Raptorial claw dactylus: 6 teeth (0); 7 teeth (1); 8 teeth (2).
9 Raptorial claw dactylus: with basal notch (0); lacking basal notch (1).
10 Telson dorsal carinae: entire (0); tuberculate (1).
11 Telson accessory median carina: present (0); absent (1).
12 Submedian teeth apices: movable (0); fixed (1).
13 Telson ventral surface lateral to postanal carina: with carinae (0); with tubercles (1); smooth (2).
14 Telson prelateral lobe: shorter than marginal carinae (0); longer than marginal carina (1); length subequal with prelateral lobe (2).
15 PLP1 endopod hook process: apex sharp (0); apex blunt (1).
16 PLP1 endopod hook process: apex not exceeding distal endite (0); apex exceeding distal endite (1).
17 Uropodal protopod: broad (0); slender (1).

Appendix 2. Input data matrix of 6 taxa and 17 characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Neoanchisquilla australiensis	1	1	1	1	1	0	1	1	0	0	1	0	2	1	0	0	1
Neoanchisquilla semblatae	1	0	0	1	1	1	0	2	0	0	1	0	2	2	1	1	1
Neoanchisquilla tuberculata	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	1
Anchisquilla fasciata	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1
Levisquilla jurichi	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0
Levisquilla minor	0	0	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0

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McEvey, S.F., J.R. David & L. Tsacas, 1987. The *Drosophila ananassae* complex with description of a new species from French Polynesia (Diptera: Drosophilidae). *Annales de la Société entomologique de France (Nouvelle serie)* 23: 377–385.

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Paterson, H.E.H., & S.F. McEvey, eds., 1993. *Evolution and the Recognition Concept of Species: Collected Writings*. Baltimore: The Johns Hopkins University Press.

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Recent Developments in Obsidian Hydration Dating

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ABSTRACT. This paper presents recent experimental results from the obsidian hydration dating research programme conducted at the Centre for Archaeological Research (CAR), Auckland University. Two elements of the essential hydration rate component are examined. First, the influence of potentially significant environmental variables other than ambient temperature is explored. Our results demonstrate that environmental variables other than temperature may have a significant influence on hydration rate, though for many archaeological situations their influence is insignificant. Second, an alternative approach to estimating the exponential mean temperatures necessary for dating is presented. It is based on modelling the soil surface energy balance. A comparison with other prediction methods shows it to be a preferable approach. Finally, the results of a blind dating applications are presented. These show that the dating method can produce results which are both sensible and useful.

JONES, M.D., P.J. SHEPPARD & D.G. SUTTON, 1998. Recent developments in obsidian hydration dating. *Records of the Australian Museum* 50(3): 235–240.

Obsidian hydration dating (OHD) involves converting a measured hydration rim thickness into a "date" based upon an estimated hydration rate. As the rate at which obsidian hydrates depends on the ambient temperature and glass chemistry (Ambrose, 1976; Friedman & Smith, 1960), accurate temperature control and an understanding of the glass reaction are fundamental to producing accurate obsidian hydration dates. This applies equally whether the OHD is produced using an independently calibrated hydration rate (a hydration rate calibrated via a primary dating technique such as a dated historic context or ^{14}C) or an intrinsic hydration rate (a hydration rate calculated on the basis of glass chemistry) (Jones *et al.*, 1997).

The purpose of this paper is to present recent results clarifying hydration rate estimation, by evaluating the influence of the hydration environment and modelling the ambient temperature regime.

Hydration rates

Hydration rates are influenced by the conditions under which the chemical conversion of obsidian into perlite takes place. Thus the rates are influenced by the environment within which the artefact is stored, and the chemical composition of the obsidian itself. Research to date has suggested that the two most important controls on hydration velocity are the storage temperature and glass chemistry (Ambrose, 1976; Friedman & Long, 1976; Michels *et al.*, 1983; Stevenson *et al.*, 1989). To verify these results a series of induced hydration experiments were conducted during 1996. One of the main questions examined in these induction experiments was "What influence do environmental variables other than temperature have on hydration rates?". This is of considerable importance to the application of obsidian hydration dating as there are

a wide number of potential reactions between obsidian and the environment that may not be taken into account in standard high temperature experimental induction programmes. While various research programmes have demonstrated the thermal dependence of hydration, the influence of other environmental variables have largely been ignored and it is possible that these factors will have a significant influence on archaeological hydration rates. In part, this is prompted by results from nuclear waste glass research that have demonstrated different rates of glass corrosion in different environments (e.g., Christensen *et al.*, 1984; Doremus, 1994; Lokken & Strachan, 1984; Shade *et al.*, 1984). Additionally archaeological research has demonstrated that surface corrosion is significant in some archaeological environments (e.g., Ambrose, 1994).

Based on this previous research it was established that the factors of pH, solute cation concentration and soil composition were likely to have an influence on archaeological hydration rates. To explore the influence these factors may have on net hydration rates an experimental induction was conducted comparing the effects of different induction media (pH, solute cation concentration and soil composition). In total nine induction media were compared, with the pH controls ranging between 3.5 and 11 (pH 3.5, 6.8, 8.0 and 10.5 using standard TRIS buffers) and the cation solute controls consisting of a brine solution ranging from 0.1 M to 2.0 M (0.1, 0.5, 2.0 M—laboratory grade NaCl solution in distilled water). As an additional experiment, the media of distilled water, silica saturated water, water vapour, soil (organic/clay mix) and silica sand were compared as induction environments. Four source samples of obsidian were used in the experiment (Table 1). They were chosen to be chemically representative of New Zealand obsidian in general and allowed any potential variation in hydration response due to glass chemistry to be outlined.

The inductions were conducted in pressure chambers maintained at a constant temperature in an incubator. Temperature measurements conducted during the hydration experiments have confirmed that the temperature within the incubator was maintained to an accuracy of ± 0.1°C. Vapour inductions were conducted by suspending freshly flaked obsidian in a pressure chamber maintained at 100% rH. The non-vapour media were contained in Pyrex beakers which had been autoclaved for four weeks at 120°C prior to the experimental run to ensure that any potentially confounding leaching reaction of the Pyrex was minimised. This experimental was conducted at 112.5°C for 8.5 days. The experimental hydration rim thicknesses were measured following the pixel intensity integration approach developed by Ambrose (1993).

The induction results (Table 2) show that there are no differences in the results obtained among inductions in distilled water, silica saturated water, water vapour, soil, silica sand, brine, or pH above 6.8. This pattern is consistent for the four obsidian sources used in the experiment, and suggests that induction experiments conducted in water vapour provide suitable data for estimating hydration rates in these media at 112.5°C.

While none of the results are statistically significant the pH experiments suggested that there was an effect generated by this environmental variable. The low pH rims were larger, as expected from similar experiments in glass science (Doremus, 1994), whereas the high and neutral pH rims gave identical results to the inductions conducted in water vapour.

Brine concentration may also have had the anticipated effect of suppressing the hydration rate, though the results are not at all significant in this study. The conclusion from these results is that solute cation concentration (< 2 M) will not have a significant effect on apparent hydration rates for hydration rim thicknesses less than 1 μm. This result may also be applicable to larger hydration rims, although our study has focussed on rims < 1 μm thick.

Table 1. Major elemental composition (Molar %) of obsidian used in the induced hydration experiments.

	Ben Lomond	Huruiki	Taumou Beach	Waiere
Si	71.01	69.85	67.09	67.24
Al	13.04	13.66	10.37	10.30
Fe	1.95	1.88	6.51	6.25
Mn	0.07	0.04	0.15	0.12
Mg	0.22	0.09	0.02	0.02
Ca	1.59	1.09	0.27	0.19
Na	6.08	6.69	8.18	8.49
K	5.68	6.40	6.94	6.70
Ti	0.22	0.11	0.26	0.17
P	0.02	0.01	0.01	0.01

Table 2. Combined percentage deviation from average thickness results for the induction media.

medium	average deviation %	standard deviation
vapour	- 2.4	4.4576
distilled water	- 2.2	4.6115
silica saturated water	- 2.2	4.3157
pH 3.5	+ 7.7	4.4361
pH 6.8	- 2.1	4.5641
pH 8	- 2.2	4.5762
pH 10.5	- 2.3	4.6829
NaCl 0.1 M	- 3.7	4.5093
NaCl 0.5 M	- 2.6	4.4404
NaCl 2 M	- 2.7	6.3323
silica sand	- 2.1	4.8820
soil	- 2.3	4.6155

The inference from this set of experiments is that obsidian that has not been exposed to pH extremes or high levels of brine will hydrate at a rate described by the hydration behaviour of glass in a saturated vapour environment (112.5°C). Fortunately the set of conditions under which hydration proceeds normally, prevail within archaeological sites in New Zealand. Though there will be problems in some tropical regions where pH extremes may exist (e.g., Sheppard & Pavlish, 1992).

Temperature

Temperature is an important governing variable in the hydration of obsidian (Ambrose, 1980, 1984; Friedman, 1976; Friedman & Smith, 1960; Jones *et al.*, 1997). As the hydration rate is exponentially related to the ambient temperature, arithmetic mean temperatures are unsuitable as estimates for the effective storage temperature (EHT) of an artefact. Many methods have been developed to provide estimates of EHT's, but they all have limitations (e.g., Jones *et al.*, 1997; Ridings, 1996).

A useful estimation model should have the following attributes:

1. *Model long term climatic trends*. Some modelling methods make use of short term data and make the assumption that this is representative of the storage history of an artefact. This will rarely be the case.
2. *Hydration model independence*. The model should be able to provide an estimate for any hydration mechanism. This is important if future research revises the current temperature dependence of the hydration reaction, and ensures *forward compatibility* of EHT estimates. Similarly the estimate should not be *analogue dependent*. Some estimations are made by measuring the mean reaction rate of an analogous system (Ambrose, 1980; Trembour *et al.*, 1988). As the exponential temperature response of these systems will be different from that of obsidian the analogue rate cannot be used in its raw form.
3. ***Model small scale temperature variation***. It has been shown that significant variations in archaeological soil temperature regimes can occur over small spatial scales (< 10m), and that this variation is driven by variables governing the surface energy balance of the soil (Jones *et al.*, 1997). A useful estimate should model these small scale variations.

None of the current estimation procedures meet all of these requirements. The procedure that most closely meets them is the use of zeolite temperature cells (Ambrose, 1980, 1984). Surveys with these devices can be designed to model small scale temperature variation, and methods have been developed to correct the estimate for the reaction rate of the analogous system (Ambrose, 1984; Chappell & Ambrose, undated). The limitation of these devices is in modelling long term temperature trends. Long term information cannot be practically incorporated into an estimate from a cell survey alone.

In response a new method based on estimating soil surface energy balances has been developed. In this model the soil surface is treated as an energy interface between the soil body and the atmosphere. The energy balance of this interface is set equal to the net external energy flux. Thus when there is more energy arriving at the soil surface than is being lost, on a hot sunny day for instance, the soil surface energy balance is positive. On the other side of this energy interface is the soil heat flux which is modelled as being driven by the soil surface energy balance. Thus when the soil surface energy balance is positive energy flows into, and is distributed throughout, the soil body. Whereas energy flows from the soil body when the surface energy balance is negative.

The temperature at any point in the soil body can be described as a function of the soil heat flux and the thermal capacity of the immediate matrix. Thus by modelling the net external energy flux we can estimate the soil heat flux through time and develop a temperature time series for any point in the soil body. This time series can be represented as a time dependent function by techniques such as harmonic decomposition and then an exponential mean temperature can be modelled for any proposed reaction mechanism.

Thus to produce an estimate we:

1. *Model the net external energy flux*. This can be a model of any degree of complexity (e.g., Ayra, 1988; Campbell, 1985; Mahrer & Avissar, 1985; Monteith & Unsworth, 1990; Oke, 1987; Stathers & Bailey, 1986; Stoutjesdijk & Barkman, 1991) incorporating all known information about long term climatic trends and responding to small scale variation.
2. *Model the soil heat flux*. This flux is dependent upon the driving external flux, and again a variety of techniques can be used to model heat flow through the

soil matrix (Campbell, 1985; Chudnovskii, 1962; Clothier *et al.*, 1986; Hanks & Ashcroft, 1980; Mahrer & Avissar, 1985; Persaud & Chang, 1984; Richter, 1987). These techniques can make allowance for variations in thermal properties of the soil matrix through different strata.

3. *Develop a temperature time series for the location.* Produce a temperature time series for the soil location.
4. *Produce an EHT.* The soil temperature time series is reduced to a time dependent equation which is integrated through time with any proposed hydration model to produce a model specific EHT.

In an evaluation of this model 10 zeolite temperature cells were placed in a meteorological station and the weight gain of these cells over a six month period was predicted on the basis of a surface energy balance integration model. The results of this prediction were then compared to the performance of other mainstream EHT estimation procedures.

Cells were placed every 10 cm from the surface to a depth of 40 cm, with two cells at each depth. The governing meteorological variables for the location were predicted via a simple ARIMA model and the soil heat flux was calculated via a numerical capacitor analogue after Campbell (1985). The resulting temperature series was reduced to a time dependent function via a 10 element harmonic decomposition and integrated via the following equation to produce a predicted cell weight gain over the survey period.

$$\Delta W = \int e^{\frac{A}{f(t)+273.16}+B}\,dt$$

A and *B* are cell hydration constants; *f(t)* is a time dependent temperature function in degrees celsius.

The predicted and actual cell weight gains have been converted to an EHT for comparison with the prediction of other estimation methods, and these results are presented in Figure 1. As can be seen, the performance of this approach to producing estimates of the recorded cell temperatures is better than the alternatives presented.

The conclusion from these results is that the energy balance integration approach is an accurate method for estimating EHT's that fulfils the requirements of a useful estimation method. The approach is not restricted to any single hydration model and can incorporate any level of complexity in the modelling of soil climate.

Case study

As a final component of this paper we present the results of a blind dating trial of obsidian from the proto-historic site of Papahinu, New Zealand (Table 3; Foster & Sewell, 1996). In this trial 39 samples of obsidian were submitted for dating where the operator was not aware of the site, association or age of the artefacts. The dates were produced by measuring the hydration rims after Ambrose (1993), and using estimated hydration rates based on the results of

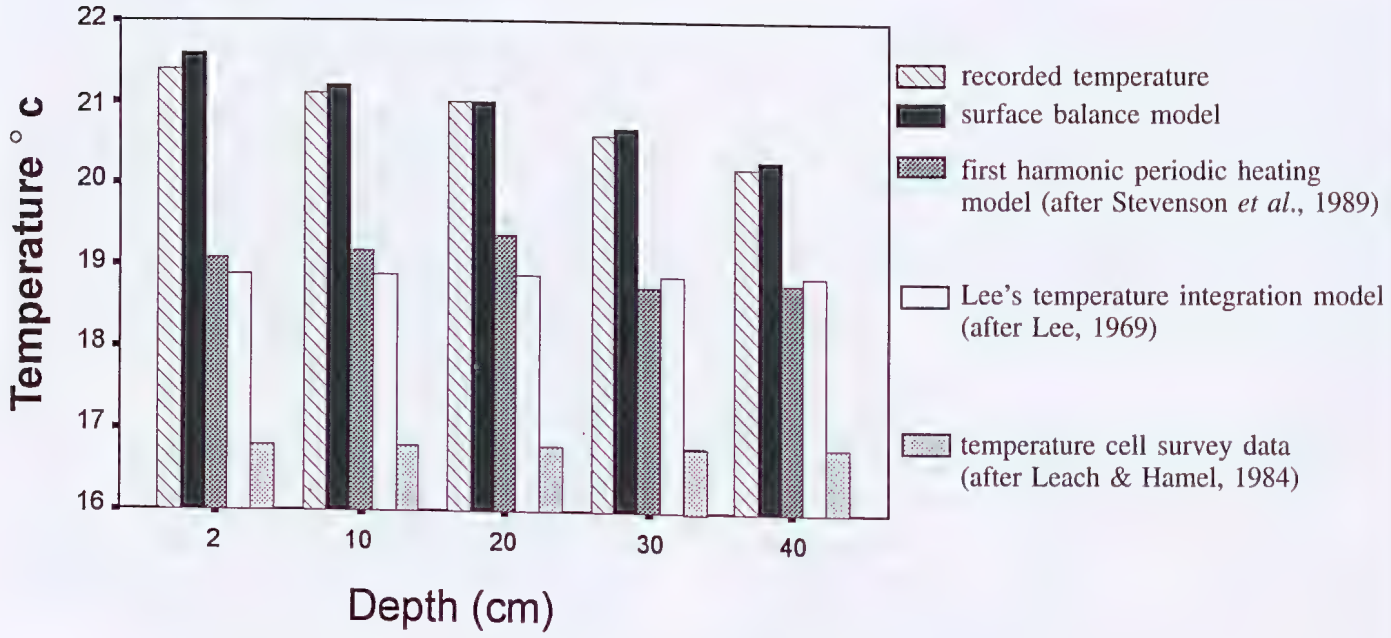

Figure 1. Recorded and predicted cell temperatures at different depths: Kumeu Meteorological Station 12 November 1995 to 14 March 1996.

Table 3. Blind dating results for archaeological obsidian from Papahinu.

lab number	description	rim (μm)	age (B.P.)	date (A.D.)	error (years)
AKU-95-74	f162	0.6	102	1848	39
AKU-95-75	nil	0.7875	176	1774	55
AKU-95-76	pit_next_to_house	0.7125	118	1832	42
AKU-95-77	house_drain	0.6	101	1849	38
AKU-95-78	f738	0.75	112	1838	38
AKU-95-79	eastern_terrace	0.825	193	1757	59
AKU-95-101	House_8_floor	0.7	106	1844	36
AKU-95-102	House_8_floor	0.6	102	1848	39
AKU-95-103	fill_firescoop	0.9	88	1862	25
AKU-95-105	fill_pit_15	0.675	129	1821	45
AKU-95-107	midden_top	0.6	102	1848	38
AKU-95-108	fill_posthole	0.75	160	1790	52
AKU-95-110	posthole_fill(early)	0.75	160	1790	52
AKU-95-112	feature_292	0.75	154	1796	50
AKU-95-113	feature_292	0.75	156	1794	51
AKU-95-114	feature_292	0.75	158	1792	52
AKU-95-115	feature_292	0.798	182	1768	57
AKU-95-117	spoil_heap	0.6	103	1847	39
AKU-95-119	spoil_heap(late)	0.675	130	1820	45
AKU-95-121	nil	0.675	130	1820	45
AKU-95-122	nil	0.5625	90	1860	36
AKU-95-123	nil	0.7875	171	1779	55
AKU-95-124	nil	0.675	129	1821	45
AKU-95-125	nil	0.675	129	1821	45
AKU-95-126	nil(early)	0.6	102	1848	39
AKU-95-127	nil	0.5625	88	1862	35
AKU-95-128	nil	0.6	96	1854	36
AKU-95-129	nil	0.525	79	1871	32
AKU-95-130	nil(early)	0.9	231	1719	67
AKU-95-131	nil	0.525	78	1872	32
AKU-95-132	nil	0.675	124	1826	43

a series of high temperature induction experiments (Jones *et al.*, undated). In total only 31 dates were produced, as eight of the samples had surface damage and were rejected. Temperature control was by the use of data generated in a regional soil temperature survey (Jones *et al.*, 1997) and the estimated EHT was 17°C. The expected date range of material from this site is from the late eighteenth century through to the mid nineteenth century on the basis of historical records and the artefacts present (Foster & Sewell, 1996; Sewell, pers. comm.). As can be seen the obsidian hydration dates for the material recovered from this site cluster tightly within the expected date range. Further more, in two cases multiple samples were submitted from single features and the date cluster from these features was very tight. In one case we have two dates within four years and in the other we have four dates within 27 years. This case study demonstrates the degree of precision and accuracy now possible with OHD in New Zealand.

Conclusion

The results presented here have demonstrated that we can describe the age of an artefact as a function of hydration rim thickness and that it is possible to control for environmental influence of the hydration rate. Further we have demonstrated that obsidian hydration dating can provide consistent dates that conform well to independently dated material. Thus we are confident that the base has been established for obsidian hydration dating to function as a useful tool for archaeology in New Zealand.

ACKNOWLEDGMENTS. The authors would like to thank the FoRST for major funding (UOA 511), Auckland University Research Committee, the Anthropology Department of the University of Auckland for continuing support. Dr R.T. Wallace and Wal Ambrose for constructive advice.

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Balmoral Beach Aboriginal Shell Midden, Port Jackson, Australia: Pumice Petrology and Sources

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ABSTRACT. Palaeopumice strand deposits (1800 to 4000 years B.P.) occur in the Balmoral Beach Aboriginal Shell Midden excavations. In composition, the pumice clasts are low-potassium dacites and contain up to 5% xenocrysts, phenocrysts and glomerophenocrysts of orthopyroxene, pyroxene, plagioclase and iron oxide minerals. The matrix includes smaller grains of these minerals in an abundant, highly vesicular rhyodacite volcanic glass. The 3300 year old and younger pumices typically contain rare xenocrysts and phenocrysts of magnesian olivine, forming an unusual mineral assemblage. One older pumice clast is a quartz-bearing rhyodacite, with distinctive trace element geochemistry. The typical dacites, resemble those erupted from the Tonga-Kermadec island arc in the Southwest Pacific, due both to the presence of olivine and the variably depleted trace and rare earth element contents. This implies a 4000 km drift caused by the East Australian oceanic current, before the pumice was stranded in Port Jackson.

SUTHERLAND, F.L., & B.J. BARRON, 1998. Balmoral Beach Aboriginal shell midden, Port Jackson, Australia: pumice petrology and sources. *Records of the Australian Museum* 50(3): 241–262.

Pumice regularly washes up on Australian coasts, usually after storm activity. In an early observation, Clarke (1842) remarked "An investigation of the range of this drift pumice along the shores of Australia and Tasmania would not be an unimportant employment". Since then, a few studies identifying pumice sources have been made. One major pumice stranding in southern Australian coasts and sub Antarctic islands, starting in late 1963, was traced to a 1962 submarine eruption in the South Sandwich Islands over 8000 km away (Sutherland, 1965; Coombs & Landis, 1966). This pumice dispersed on the southern polar currents may have even circumnavigated the Southern Ocean to restrand as fine pumice gravel on Australasian coasts by mid-1965 (Sutherland & Olsen, 1968). More recently, studies of pumice stranded on cays and beaches along North Queensland have suggested Southwest Pacific sources, mostly from the Tonga-Kermadec island arcs some 4000 km away (Bryan, 1968; Stanton, 1992). This pumice travels on the South Equatorial Current, east to west from Fiji to the Coral Sea. Here the current splits and the main branch runs north to south along the Australian shelf deflecting off southern New South Wales to run from west to east (Rotschi & Le Masson, 1967; Tomczak & Hao, 1989; Burrage, 1993). Thus, Southwest Pacific sources could be expected to supply a large proportion of the pumice washing up on New South Wales coasts (Fig. 1). Extended sources could be involved as the tropical convergence separating the east to west flowing South Equatorial Current from the returning west to east currents ranges from 18–25°S (cf. Martinez, 1994, and Nelson *et al.*, 1994).

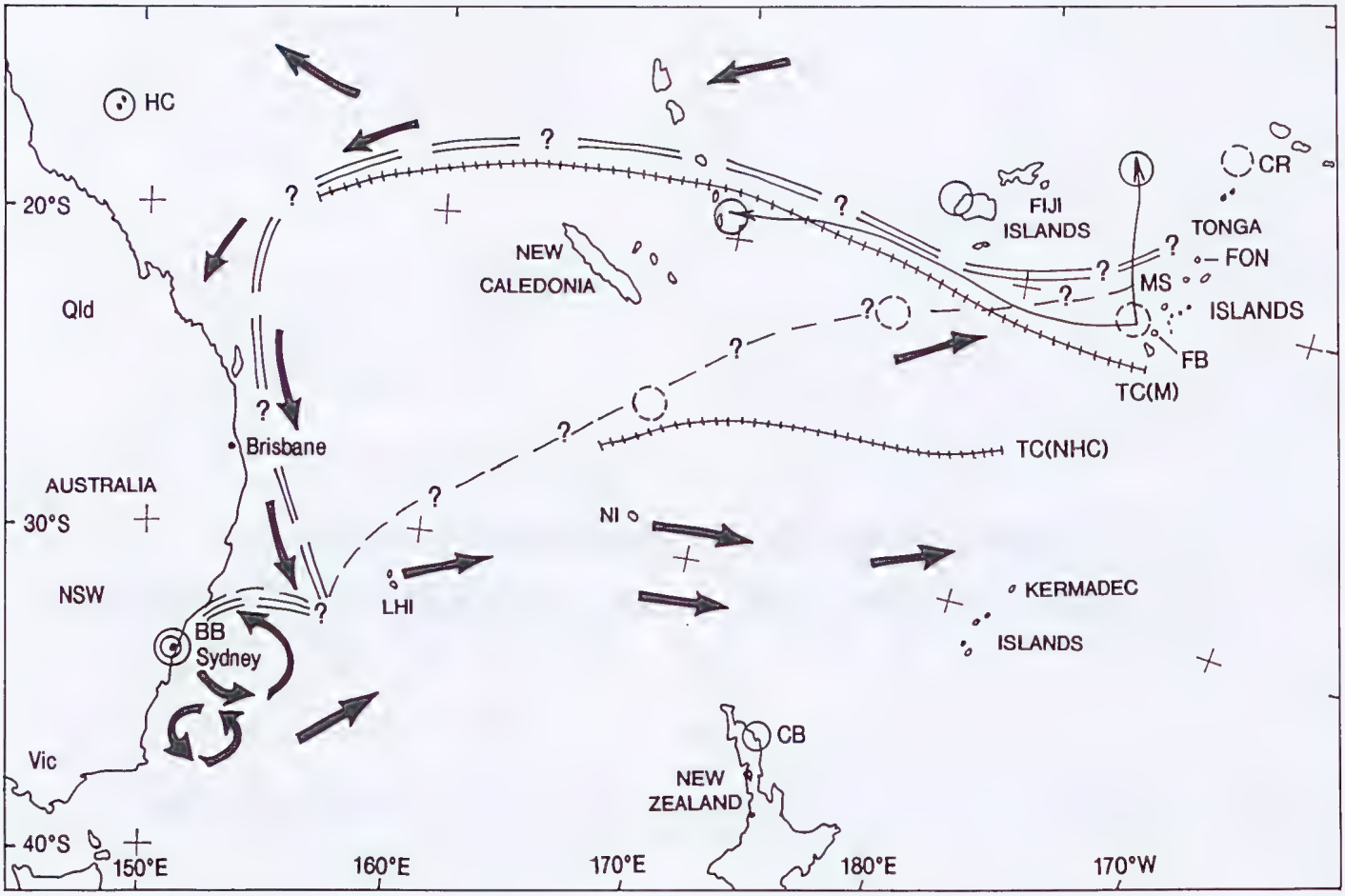

Figure 1. Map of eastern Australia-southwestern Pacific region after Bryan (1968), showing locations of pumice sightings (dashed circles) and pumice strandings (complete circles), with the 1928 Falcon Bank (FB) pumice eruption sites linked by thin arrowed lines and Balmoral Beach (BB) palaeopumice site indicated by double circle. Other sites include Fonualei dacite volcano (FON), Metis Shoal (MS) Curaçoa Reef (CR), Herald Cays (HC), Cape Brett (CB), Norfolk Island (NI) and Lord Howe Island (LHI). The two positions shown for the Tropical Convergence (hatched lines) follow Martinez (1994), symbolised TC (M), and Nelson *et al.* (1994), symbolised TC (NHC). Main surface current flow directions are indicated by heavy arrows, while two alternative routes for Balmoral pumice drift from a potential North Tongan source are indicated by double dashed and single dashed lines.

Major submarine pumice eruptions occur repeatedly from the Tonga-Kermadec volcanic arc and the pumice usually drifts through Fiji and New Caledonia before reaching East Australian coasts about a year later (Jokiel, 1990). These eruptions not only introduce exotic pumice onto Australian coasts, but the pumice also transports exotic coral juveniles from far east and south east regions into the Great Barrier Reef off Queensland, which helps to build up the coral diversity. The many submarine pumice eruptions from island arcs bounding the eastern Australian plate margin combined with the prevailing east to west current flows from these regions produce the considerable range of pumice compositions found within Australian Holocene beach deposits (e.g., south eastern Queensland coasts; Little & Ward, 1980). The ability of Southwest Pacific pumice to travel considerable distances is documented by drift pumice from a submarine Tonga Trench eruption appearing in the Indian-South Atlantic Ocean region (Frick & Kent, 1984). Catastrophic caldera pumice eruptions are also recorded in the last 4000 years from the North New Zealand-Kermadec-Tonga volcanic zone (Taupo, New Zealand [Pullar *et al.*, 1977]; Raoul Island [Lloyd & Nathan, 1981]); these can release large quantities of sea-rafted pumice. Some of these sea-borne pumices could reach Australian coasts, depending on past current patterns.

As well as historic pumice strandings, pumice layers also appear in prehistoric Holocene raised beach deposits on eastern Australian coasts, e.g., North Bulli raised beach deposits at 4 m a.s.l. dated at 5200 ± 2000 years (Bryant *et al.*, 1992a). Profuse pumice also appears in later disturbed beach deposits, interpreted as possible tsunami effects in the last 3000 years (Bryant *et al.*, 1992b). However, petrological studies and detailed sources for such pumices are not yet reported. Archaeological excavations at the Balmoral Beach Aboriginal midden site within and outside a rock shelter in Port Jackson, revealed pumice-bearing layers within the sequence dated between 1800 to 4000 years B.P. The main pumice layers were dated at 3280 ± 60 B.P. and 3250 ± 90 B.P. using radiocarbon determinations

on associated charcoal and these layers lie close to present sea level (Attenbrow *et al.*, 1997; Attenbrow & Hashimoto, in prep.).

This paper describes the petrology of pumice pieces sampled from the main pumice horizon and from sparser pumice in horizons below and above this main pumice horizon.

Analytical methods

Pumice pieces were sectioned for microscopic examination and analysis of contained crystals and glass matrix. From this analytical base, comparisons were made with pumices of similar petrology described in the literature, particularly pumice described from Southwest Pacific regions, to suggest potential sources.

Seven pumice samples were examined. P1, P2 and P5 came from the main 3300 year old pumice layer, with P1 and P5 coming from outside the rock shelter and P2 from inside the rock shelter. P3, P6, P7 came from lower, earlier levels in both sites that are dated between 3300 and 3500 years, while P4 came from higher later levels dated between 1800–2800 years.

Pumice samples were viewed under a stereo-microscope and polished thin sections of selected pieces were studied using a polarising petrological microscope, prior to electron microprobe (EMP) analysis. Compositions of mineral grains and glassy matrix were made on a CAMECA S X 50 Microprobe, at Macquarie University, Sydney, using an accelerating voltage of 15 kV and a beam current of 20 na, measured in a Faraday cup. Precisions were better than ± 1% for elements over 10 wt% oxide, ± 5% at 1–10 wt% levels and ± 10 at levels below ± 1 wt%. Bulk whole rock analyses of pumice were not attempted due to uncertainties of contamination and leaching effects in the more altered glass. However, approximate bulk analyses were calculated by combining mineral mode compositions with fresh glass analyses.

Trace elements, including Rare Earth Elements (REE), were analysed from four pumice glasses using laser ablation and Induced Coupled Plasma Mass Spectrometry (ICPMS) at Macquarie University, Sydney (Norman *et al.*, 1996). The laser source used a Continuum Surelite I-20Nd:YAG laser, with wavelength 266 nm, Q-switch delay of 230 µsec., frequency of 2 Hz, power of 2 mW and energy of 1 mJ/pulse. The ICP-MS used a Perkin Elmer ELAN 5100 spectrometer, with a peak hop scanning mode, 50 msec. dwell time, 1 sweep/reading and between 20–60 replicate analyses. The Calibration Standard was NIST 610 glass and the Internal Standard was Ca44. The accuracy in element values increases with count time, so that the lower count times were not considered among the final analyses used for plotting results.

Pumice description

Features of the samples P1 to P7, their mineral contents and glass type are summarised in Table 1 and hand specimen and polished, thin-section descriptions of the pumice samples can be obtained from the authors. All pumices include mineral xenocrysts, phenocrysts and glomerophenocrysts that make up between 1–5 volume percentage of the rock. Minerals commonly include plagioclase, clinopyroxene, orthopyroxene and opaque iron oxides, but four of the seven pumices contain olivine (P1, P2, P4, P5) and one olivine-free pumice contains phenocrystic quartz (P7). Olivine and clinopyroxene appear in both xenocryst and phenocryst forms (Figs. 2, 3) and glomeroporphyritic groups commonly contain pyroxenes (Fig. 4) and plagioclase (Fig. 5). Some phenocrysts show magmatic corrosion, inclusions of glassy melt and intergrowths with opaque oxides and even apatite (Fig. 6). Quartz microphenocrysts appear in only one sample (Fig. 7).

Pumice clasts are generally extensively vesiculated, with voids forming 60–80% of the rock. In some pieces voids show changes in flow alignment and flattening, suggesting aggregates of spatter (Fig. 8). The pumice may be partially altered making refractive index determinations of matrix glass problematical. However, all fresh glasses analysed by EMP were silica-rich in the range of rhyodacite-rhyolite (71–77 wt% SiO_2). Most pumices contain a range of xenocryst/phenocryst minerals, with plagioclase (50–55%) dominating over orthopyroxene (15–30%) and clinopyroxene (10–20%), and opaque oxides (10%) and olivine (2–5%) forming accessory roles. However, P3 is dominated by orthopyroxene and clinopyroxene phenocrysts with only sparse plagioclase and oxides.

Analytical results

Representative compositions of pumice minerals for P1, P4–7 are given in Table 2 and are plotted in standard chemical variation diagrams in Fig. 9.

Mineral compositions. Calcian plagioclase dominates phenocrystic feldspar in most pumices (Fig. 9A). Zoning in some phenocrysts trends from calcian (core) to more sodian (rim) compositions. Microphenocryst and groundmass compositions as calcian as bytownite appear in one pumice (P6), while xenocrysts and phenocrysts as sodian as andesine associated with a labradorite-bearing groundmass appear in another (P1).

Orthopyroxene compositions are moderately iron-rich (Mg_{50-60} Fe_{35-40} Ca_{0-5}). Clinopyroxenes include both diopside and augite (Fig. 9B) and both can occur together (P2, P5). The diopside shows zoning from more magnesian cores to more iron-enriched rims and olivine shows two distinct compositions (P1, P2; Fig. 9B). A xenocryst/resorbed phenocryst (Fig. 9C) of magnesian olivine (Fo_{89-91}) contrasts with more iron-enriched phenocrystic olivine (Fo_{82-83}).

Opaque iron oxides are dominated by members of the magnetite-ulvospinel series and include near end-member magnetite and two titanian ulvospinel phases (Fig. 9D). The main layer pumices (P1, P2, P5) contain both magnetite and the more titanian ulvospinel and minor ilmenite, while other pumices typically contain an intermediate titanian ulvospinel.

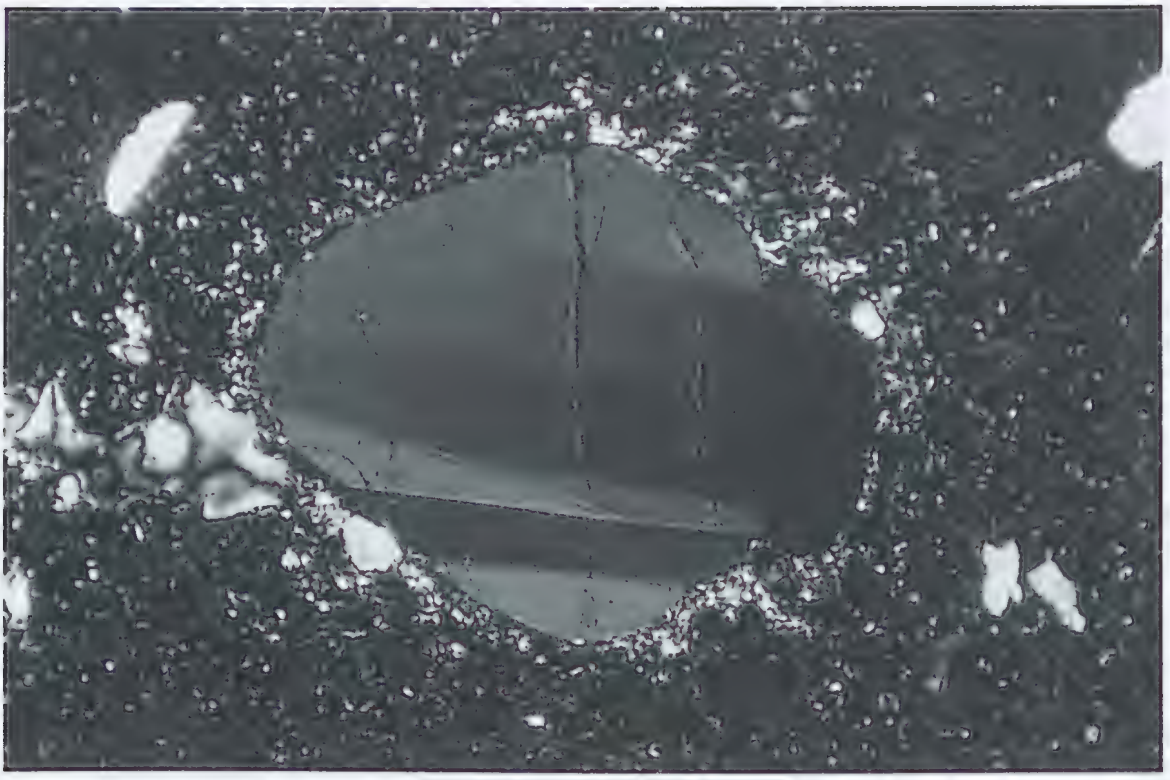

Figure 2. Olivine xenocryst (1 mm long) showing strain lamellae in vesicular volcanic glass (Pumice P1). Cross polarised light. (Photomicrography—B.J. Barron).

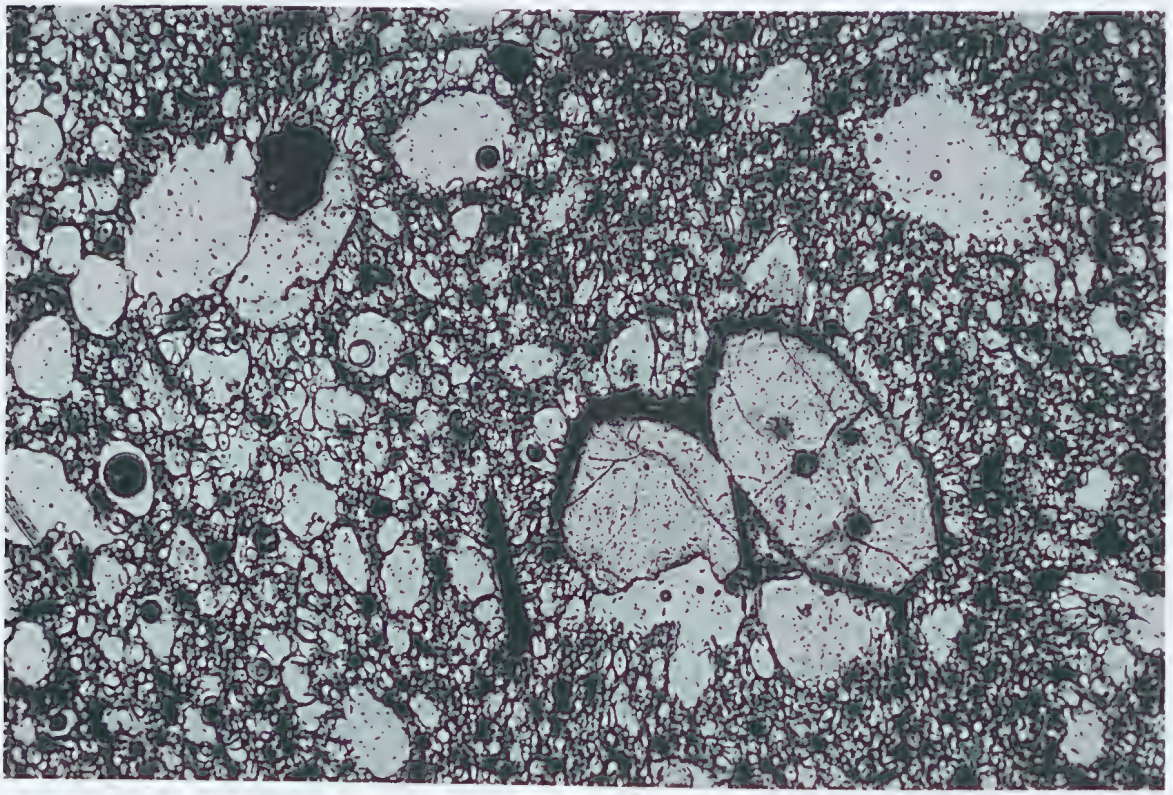

Figure 3. Olivine phenocrysts (up to 0.5 mm long) and small plagioclase-opaque iron oxide glomerophenocryst in vesicular volcanic glass (Pumice P2). (Photomicrography—B.J. Barron).

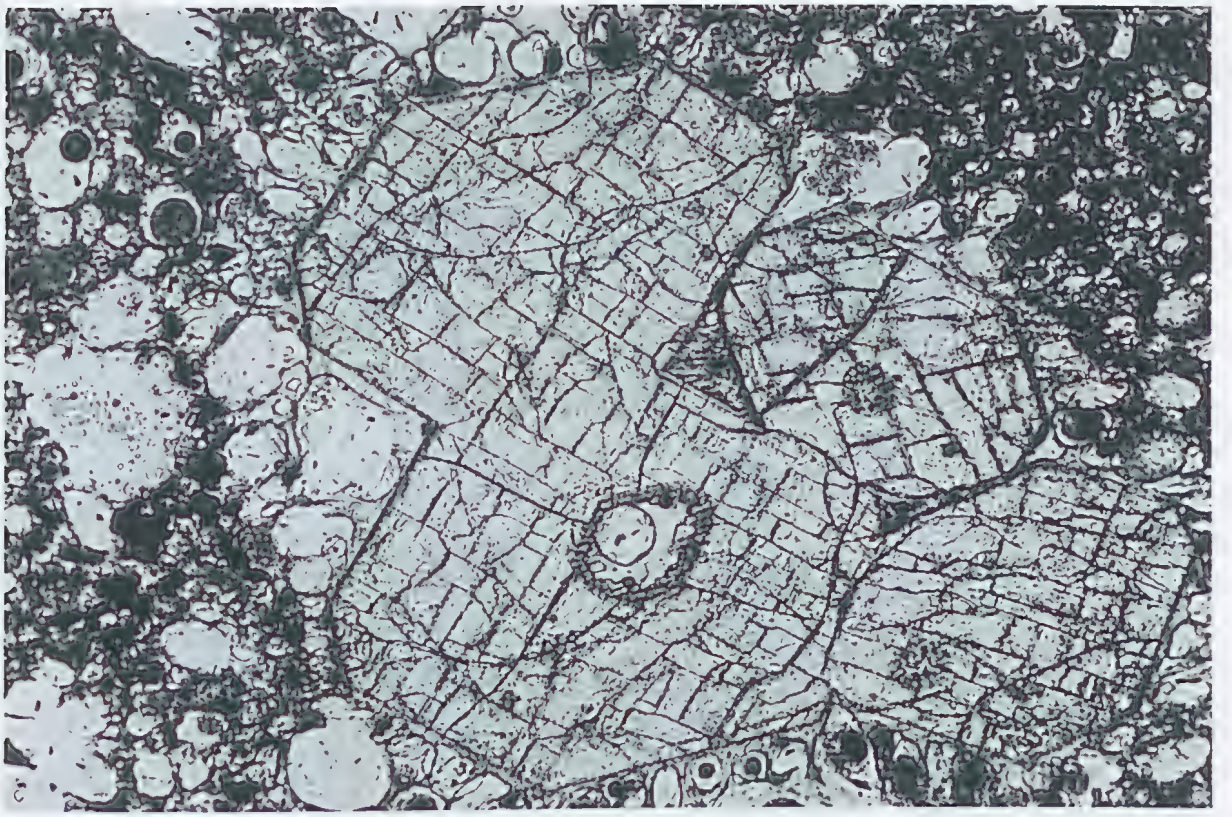

Figure 4. Clinopyroxene glomerophenocrysts in vesicular volcanic glass (Pumice P1). The largest double crystal (0.6 mm across) contains a rounded volcanic glass inclusion with a rim of minute amphibole(?) crystals. Plane polarised light. (Photomicrography—B.J. Barron).

Figure 5. Plagioclase glomerophenocrysts (cluster 0.8 mm across) surrounding a pale green orthopyroxene crystal (0.3 mm long) in an intensely vesicular volcanic glass (Pumice P1). The plagioclase crystals contain fluid inclusions and the orthopyroxene crystal contains an inclusion of brown volcanic glass and an opaque oxide. Plane polarised light. (Photomicrography—B.J. Barron).

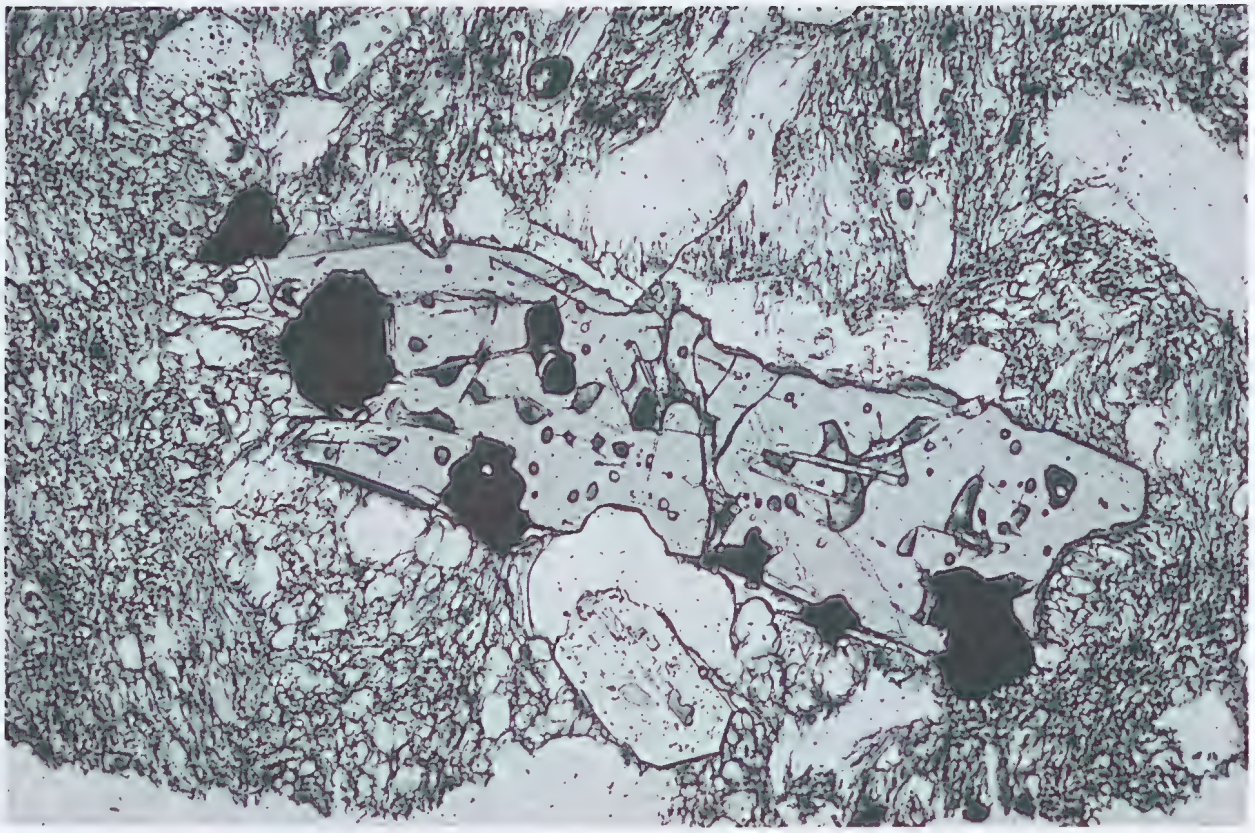

Figure 6. Orthopyroxene phenocryst (1.4 mm long) in vesicular volcanic glass (Pumice P5). The pale green orthopyroxene crystal is somewhat corroded and encloses abundant inclusions of opaque iron oxide, apatite needles and pale brown volcanic glass. Plane polarised light. (Photomicrography—B.J. Barron).

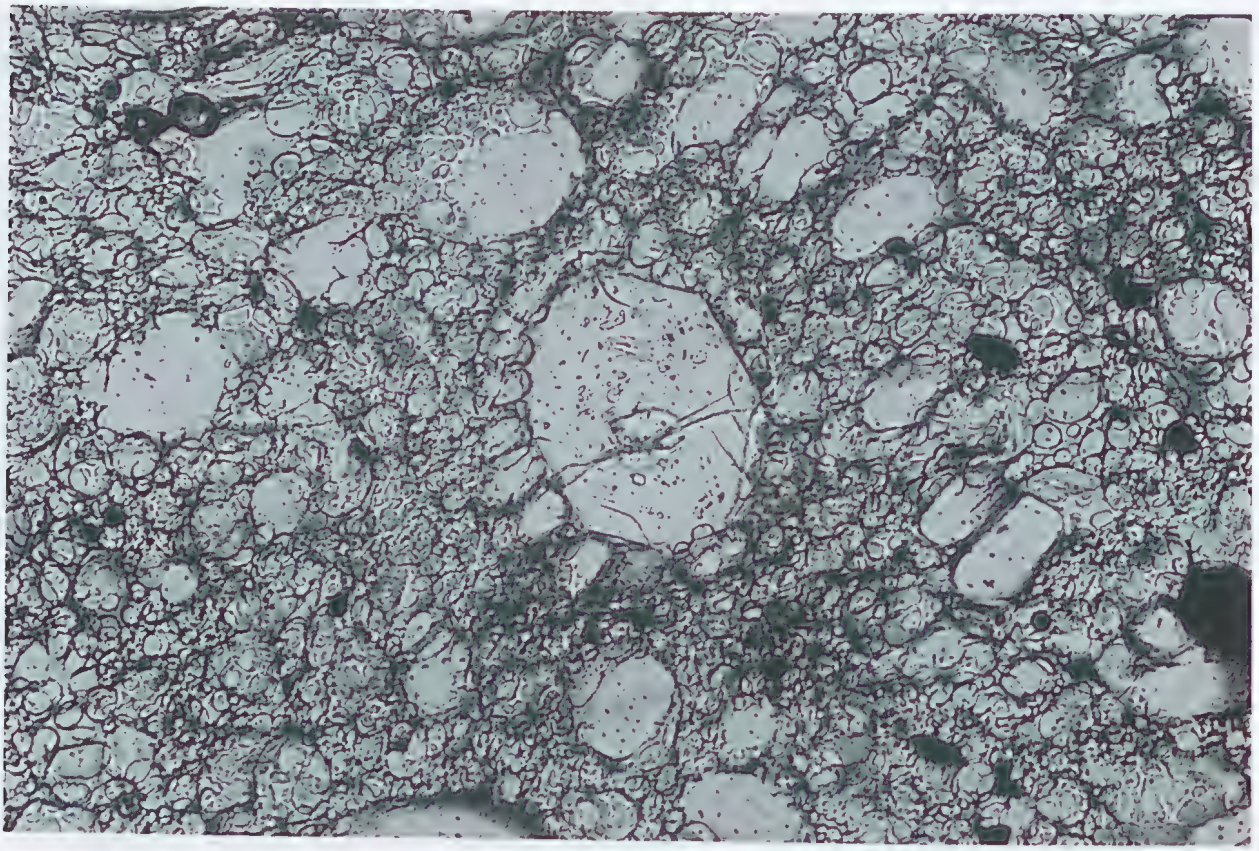

Figure 7. Quartz phenocryst (0.2 mm long) in intensely vesicular volcanic glass (Pumice P7). Part crossed polarised light. (Photomicrography—B.J. Barron).

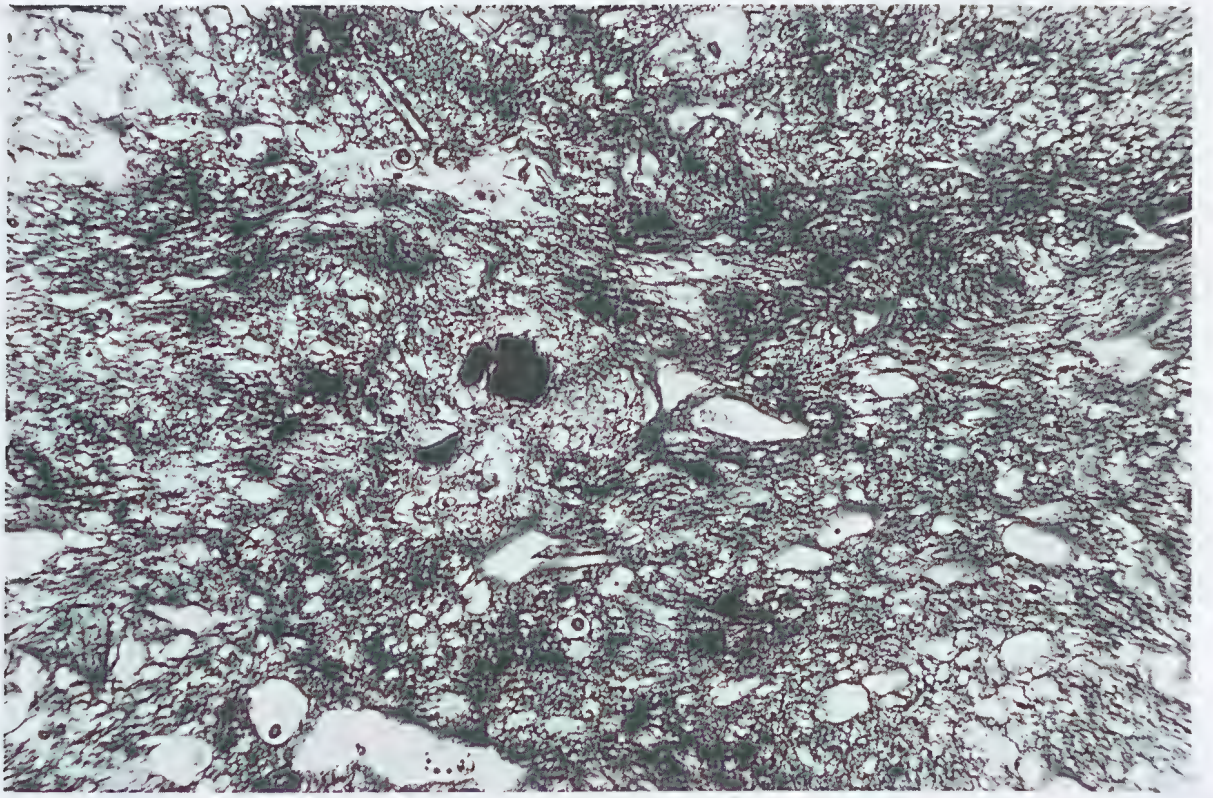

Figure 8. Vesicular volcanic glass (Pumice P3) showing somewhat chaotic eutaxitic texture and partial oxidation from weathering. The field of view is 2.8 mm in long dimension. Plane polarised light. (Photomicrography—B.J. Barron).

Glass compositions. Representative glass compositions for pumice matrix fractions and for glass included in pyroxenes are presented in Table 3, with their calculated anhydrous CIPW norms. All glasses are silica-rich, with low alkalis and relatively sodic compositions. They are quite rich in normative calcian plagioclase and also show minor normative corundum. Glass inclusion compositions overlap matrix glass compositions and form trapped melt. All glasses represent evolved melts, ranging from D.I. 67–75 and Mg number 18–28 (Table 3) and showing high normative quartz (Fig. 9E). They pass into rhyodacitic compositions (over 69 wt% SiO_2; Wilson, 1989). The appearance of quartz and corundum together in the norm probably reflects low alkalis (Hughes, 1982: 101), so that all calcium is combined with aluminium to form plagioclase. This would leave insufficient calcium to form normative diopside, present in small amounts in other comparable rhyolitic glasses (0.6–3.3% di; Table 3).

Trace elements. These were determined on matrix glass from four pumice samples and as the glass is 4 to 5 times more abundant than the phenocrysts the analyses provide useful signatures to characterise pumice differences. Representative laser ablation ICP-MS results for Large Ion Lithophile (LIL), High Field Strength (HFS) and Rare Earth (RE) elements are listed in Table 3 and their chondrite-normalised patterns are compared in Fig. 10.

All patterns show spiked profiles predominantly with values enhanced compared to the chondritic mantle, following chondrite values used by Taylor & McLennan (1985). A notable trough is present for Nb relative to Zr in the HFS elements and peaks for Ba and U appear in the LIL elements. The REE patterns are relatively flat and a noticeable Eu depletion only appears in the main layer pumice (P2). Each pattern however is distinctive, showing variation in Th, Sr, Nd, Hf, Pr, Y and Pb enrichments and depletions. The quartz-bearing pumice (P7) is markedly different, in its relatively higher Rb, Th, Pr and Pb.

Pumice characterisation

The pumices contain rhyodacitic glass (over 69 wt% SiO_2) as their major component. However, these residual compositions do not reflect their bulk compositions, as these will be modified by the xenocryst/phenocryst contents. Bulk analyses of pumices were not made, as alteration in the pumices would lead to misleading results. However, approximate bulk major element compositions can be estimated by combining the remnant fresh glass composition with mineral compositions of the included crystals. Calculated bulk compositions for pumice samples P1 and P2 in the main pumice layer are given in Table 5. Relative to K_2O, these show a general decrease in SiO_2 and increases in FeO (total), CaO and MgO, with relatively minor increases in Al_2O_3 and in Na_2O. The estimates of the bulk compositions correspond to low-potassium dacites (63–69 wt% SiO_2).

The pronounced Nb depletion relative to Zr and strong Ba and U enrichment in the chondrite-normalised trace

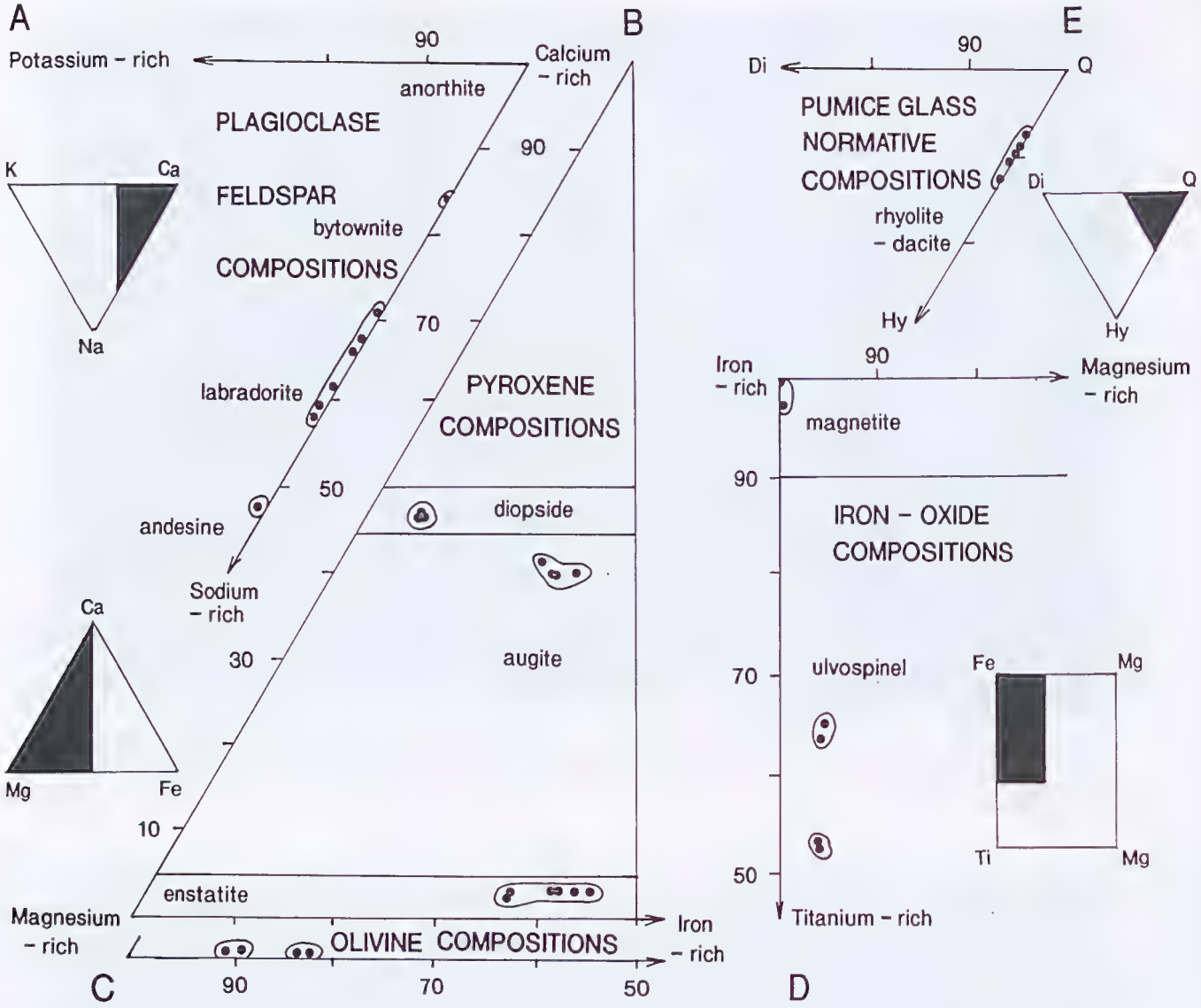

Figure 9. Mineral and glass composition plots (solid dots within circled fields) for Balmoral Beach pumices, with mineral cation data taken from Tables 2A–2D and normative glass data from Table 3. A, plagioclase feldspar compositions plotted in a Ca-Na-K triangular diagram; B, pyroxene cation plots in an Mg-Ca-Fe triangular diagram; C, olivine cation plots in an Mg-Ca-Fe triangular diagram; D, iron oxide cation plots in an Fe-Mg, Fe-Ti, quadrilateral diagram; E, normative pumice glass plots in a di-qz-hy triangular diagram. Note the plots do not include potential small diopside components, due to possible minor deficiencies in alkalis.

elements in the pumice glasses are features typical of island arc rocks (Wilson, 1989: 172–180). However, low alkalis are characteristic, especially potassium, in Balmoral pumices. The low-K presumably is linked to the depleted Rb and sometimes Sr found in these glasses. Such low-K dacites, rhyodacites and rhyolites, lacking hydrous phenocryst phases, are typical of evolved rocks erupted from the Tonga-Kermadec island arc (Melson *et al.*, 1970; Bryan *et al.*, 1972; Ewart & Bryan, 1973; Ewart *et al.*, 1973, 1977; Bryan, 1979; Ewart & Hawkesworth, 1987) and are also found among glasses in the Lau Basin volcaniclastic record since 5 Ma (Clift & Vroon, 1996). These features also characterise drift pumice that reaches the east Australian coast (Bryan, 1968) and comparative trace element and bulk analyses of the Balmoral pumice, Coral Sea drift pumice, Tongan dacites and Lau Basin rhyodacitic glasses are given in Tables 4 and 5.

Temperatures of crystallisation for early phenocrystic, olivine and diopside in pumices P1 and P2 were calculated from their mineral compositions, using the newly developed olivine-clinopyroxene geothermometer of Loucks (1996). These give temperatures between 980–1040°C which overlap with those determined for Tongan basaltic andesites from pyroxene equilibration thermometry (992–1125°C; Ewart *et al.*, 1977). The calculated temperatures, however, may not directly relate to the host dacite, as these phenocrysts may be basaltic in origin; many Tonga-Kermadec arc felsic magmas contain phenocryst assemblages that can be interpreted as resulting from accidental inclusion of basaltic crystals (I.E.M. Smith communication, 1997). Co-existing pyroxenes in pyroxene-plagioclase glomerophenocrysts (pumice P2) give temperatures between 890–960°C (Fe^{3+} recalculated compositions) based on two-pyroxene thermometry of

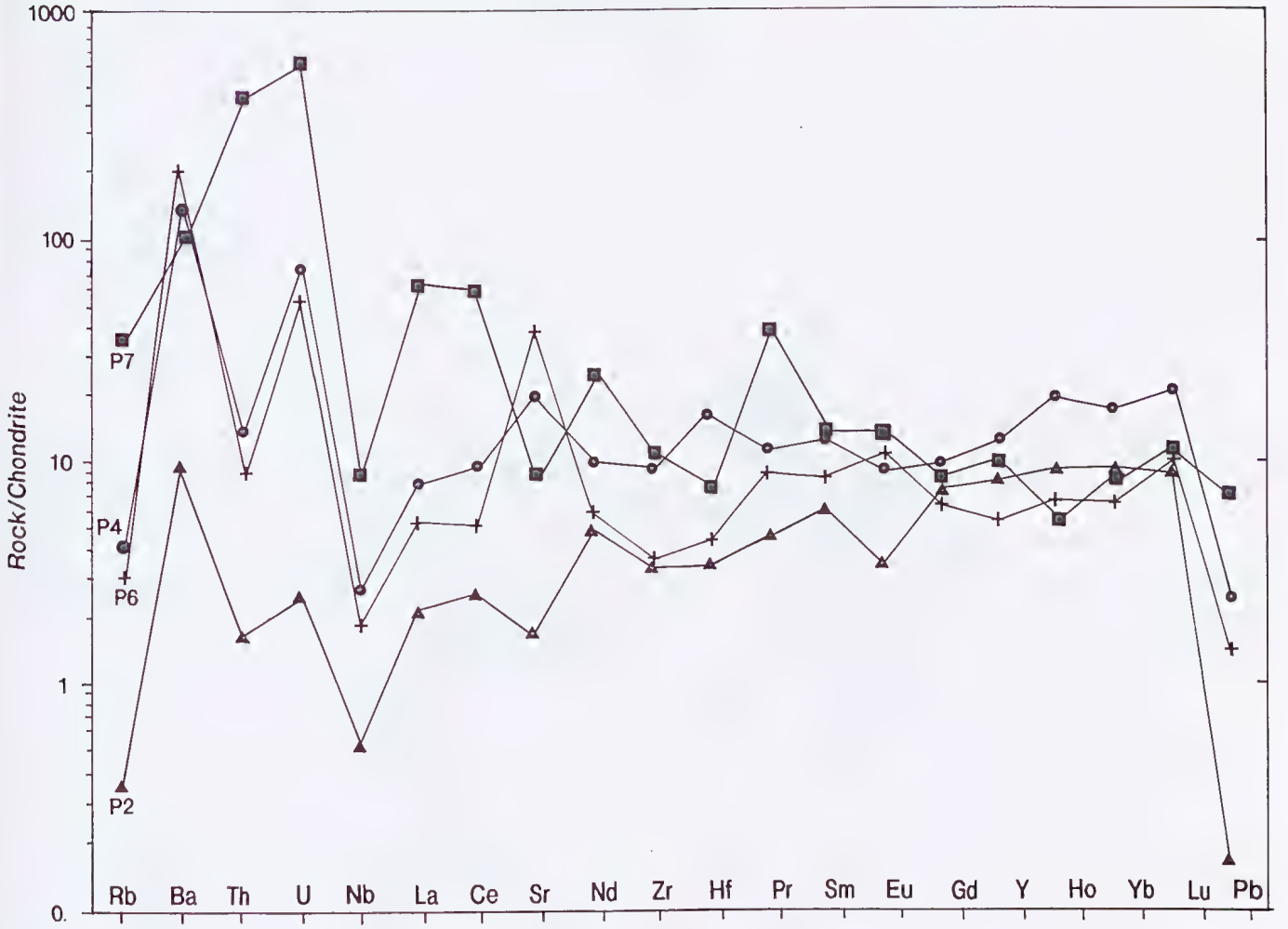

Figure 10. Incompatible and rare earth trace element chondrite-normalised plots (chondrite values after Taylor & McLennan, 1985) for representative pumice pieces, with P2 (triangles) from main pumice layer, P4 (solid dots) from later pumice layers and P6 (crosses) and P7 (solid squares) from earlier pumice layers. Trace element values normalised from Table 4.

Wood & Banno (1973) and Wells (1977) and these lie in the temperature range of 764–1150°C estimated for Tongan dacites from plagioclase thermometry at water pressures between 1–5 kb (Ewart *et al.*, 1973).

An unusual feature of pumices from the main and later layers (P1–2, P4–5) is the presence of xenocrysts/phenocrysts of magnesian olivine associated with a rhyodacitic glass. This characteristic is recorded in the Southwest Pacific area only from the Tongan islands, e.g., Metis Shoal (Melson *et al.*, 1970), so the 3300 year old and later Balmoral pumices may have originated from this region.

Discussion

The general similarities in phenocryst mineralogy and glass compositions for much of the Balmoral pumice suggests they came from a related source region. Low alkalis, with low K_2O are typical of Tonga-Kermadec arc rocks, although the Balmoral pumices seem particularly poor in alkalis (Table 6). Some alkalis may have preferentially volatilised during EMP analysis of the Balmoral glasses, as sodium loss can occur (Reed, 1975: 182–185). However pronounced loss is unlikely in this case, with use of a defocused beam. The low Rb and incompatible elements in most of these glasses suggests that any K loss was relatively limited. The rare quartz-rhyodacite pumice (P7) from pre-3300 year levels shows a distinctly different trace element pattern to the other rocks, which may reflect a separate source region. This pumice glass has the highest K_2O (1 wt%) and has significantly lower K/Rb (29.5), higher Rb/Sr (0.83) and greater Ce (111 ppm), La (84 ppm) and Zr (178 ppm) contents than observed in the other pumices. In these characteristics it resembles rhyolites and dacites that are erupted through continental crust, as in North Island, New Zealand, (K/Rb < 270, Rb/Sr > 0.2; Ewart *et al.*, 1973, 1977).

Tongan Arc sources. The discrimination between potential Tongan or Kermadec sources for most Balmoral pumices is somewhat problematical. Tongan dacites are generally enriched in iron relative to alkalis compared to Kermadec dacites (Ewart *et al.*, 1977). Thus, Balmoral dacites appear closer to the Tongan field (Fig. 11). However, the Metis

Figure 11. Total alkalis (Na_2O+K_2O)-FeO-MgO wt% variation diagram, showing plots of Balmoral Beach, Herald Cays and Metis Shoal dacite compositions in relation to Tonga (T), Kermadec (K) and New Zealand (NZ) dacite fields. Balmoral Beach bulk compositions (BB dashed field) connected to Balmoral main pumice glass compositions (BM enclosed dots), Balmoral later pumice glass composition (BL enclosed dot), Balmoral earlier pumice glass compositions (BI enclosed crosses), Herald Cays dark (square) and light (inclined cross) pumice compositions (HC tie line), Metis Shoal bulk (triangle), and glass (star) pumice compositions (MS tie line). Compositions from Tables 3, 5 and 6 and Southwest Pacific-New Zealand dacite fields from Ewart *et al.* (1977).

Shoal dacite and glass from Tonga plot near the Kermadec field (Ewart *et al.*, 1973). Also, any loss of alkalis from Balmoral glasses during EMP analysis, would shift plots towards the Kermadec and Metis Shoal fields.

Ewart & Hawkesworth (1987) plotted Al_2O_3/TiO_2 against CaO/TiO_2 and showed that, providing plagioclase accumulation effects were compensated for, both Al_2O_3/TiO_2 and CaO/TiO_2 decreased systematically along the arc from north Tonga to south Kermadec. Plots of Balmoral compositions are compared with plots from Fonualei Island and Metis Shoal, Tonga, from the Kermadec islands and from other east Australian low-K drift pumice in Fig. 12; note that these above oxide ratios will not be affected by any potential loss of alkalis from the Balmoral analyses. The Metis Shoal bulk analysis, with some 9% plagioclase phenocryst content, is well separated from its glass composition. However, compensation for any plagioclase accumulation effects would shift compositions towards the glass plots. Balmoral pumices contain much less plagioclase phenocrysts (2–3%) and the estimated bulk plots lie closer to the glass plots. This suggests that the bulk plots would require little adjustment for plagioclase accumulation. When plagioclase compensation trends are applied to the Tongan and Kermadec dacitic fields, similar

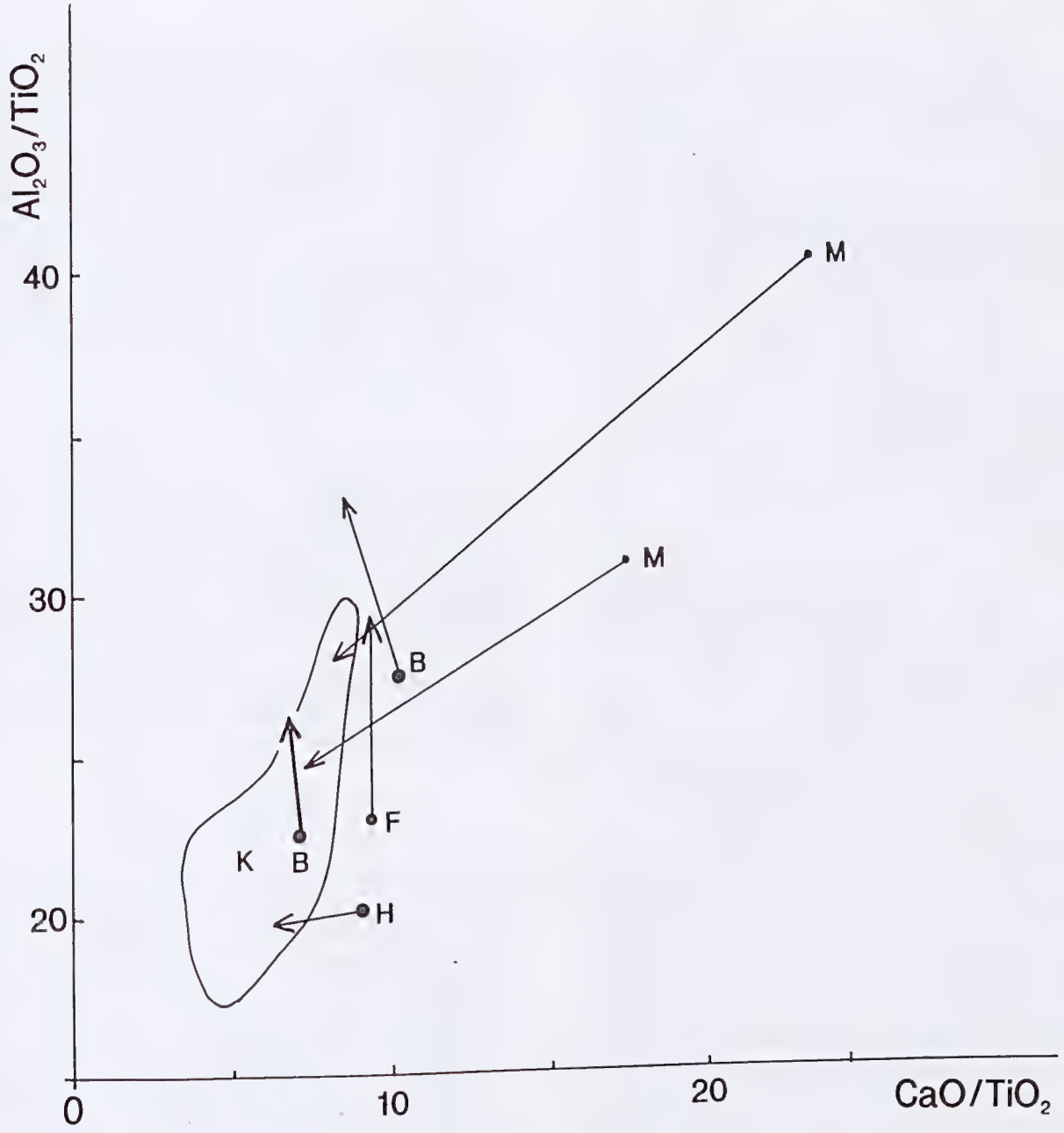

Figure 12. Al_2O_3/TiO_2 versus CaO/TiO_2 wt% variations diagram, showing trends for Balmoral Beach main pumice calculated bulk and glass compositions (B heavy dot arrow), Metis Shoal bulk dacite and glass composition (M light dot arrows), Fonualei bulk dacite and matrix composition (F light dot arrow), Herald Cays dark and light pumice compositions (H light dot arrow), in relation to Kermadec dacite field (K). Data from Tables 3, 5 & 6, with Kermadec dacite field based on analyses from Ewart *et al.* (1977).

to those for the basalt and basaltic andesite fields, then Balmoral glasses plot closer to Tongan than Kermadec fields. There are differences in the evolutionary trends for individual dacite-matrix pairs in this variation diagram. Thus, Balmoral and Fonualei trends increase in Al_2O_3/TiO_2, while Metis Shoal and Herald Cays trends decrease in Al_2O_3/TiO_2, suggesting a similar evolution for Balmoral and Fonualei dacites.

The main Balmoral pumice glass (P2) is notable for its extremely depleted incompatible element pattern. The values (ppm) for Nd (3.5), Sr (21), Ba (33) and Zr (18) are comparable to those in Mid-Ocean Ridge Basalts (Ewart & Hawkesworth, 1987), where average depleted and normal MORB values show Nd (2–8), Sr (40–140), Ba (1–20) and Zr (14–90). Considerable variations in incompatible element values exist between this depleted Balmoral pumice and other Balmoral pumices (see Table 4 and Fig. 10). Excluding the unusual pumice (P7), Balmoral pumices range in Nd (3–7), Sr (21–388), Ba (33–643) and Zr (18–50). Such variable enrichments are a feature of the Tonga-Kermadec arc (Ewart & Hawkesworth, 1987; Ewart *et al.*, 1998), where the greatest HFS-element depletions appear at the north end. This would favour a northern Tonga source for most Balmoral pumices.

Over the past 150 years, the only recorded source of olivine-bearing low K-dacite in the Southwest Pacific region is at Metis Shoal (Melson *et al.*, 1970). However, activity here may not have produced the main Balmoral

pumice, as incompatible trace elements for the 1967–1968 eruption dacite are far more enriched (Ewart *et al.*, 1973; Kay & Hubbard, 1978) compared to the depleted Balmoral glass (Table 4). A Metis Shoal source therefore would need considerable source enrichment over a 3300 year evolution. The later olivine-dacite (P4) is closer to Metis Shoal dacite in its trace element pattern. A more northern HFS-depleted Tonga source is proposed for the main pumice, particularly as submarine pumice rafts also emanate from the extreme north of the Tongan arc (Curaçoa Reef; Latter, 1976). The Ba/Th ratio (330) and low Nd (3.5 ppm) for the main Balmoral dacite (P2) are compatible with values for the northern Tafahi-Niuatoputapu island group, while higher Ba/Th (792–1608) and Nd (4–7.1 ppm) values for other Balmoral dacites (P4, P6) are more compatible with Tongan island sources lying south of this group (Turner & Hawkesworth, 1997).

Alternative sources. Oceanic current flows off eastern Australia may have varied over the last 2000–3000 years, so sources other than Tonga are possible, e.g., Kermadec sources. However, on present current flow directions, pumice from Kermadec sources would encounter prevailing east to west current flows related to the return flow of the East Australian Current. Other possibilities include sources around the Fiji, Vanuatu and Norfolk Basins, where pumice sightings and strandings are also recorded (Bryan, 1968; W.R. Dickinson, pers. comm. 1997). However, pumice (W.R. Dickinson sample) from a palaeostranding at Sigatoka, Fiji, of similar age range to the Balmoral strandings appears petrologically distinct to the Balmoral material. Low-K silicic rocks are found in a few Vanuatu centres (Carney *et al.*, 1985; Peate *et al.*, 1997), but are relatively lower in silica (< 64 wt% SiO_2) than the Balmoral, Herald Cays and Tongan dacites. Pumice sources further north in the Solomon, Bouganville and New Britain island arcs also need consideration. Drifts from these sources, however, would meet northward flowing circulation of the Hiri Current, the northerly extension of the Southern Equatorial Current (Burrage, 1993) and so would be impeded in reaching New South Wales coasts.

The main Balmoral palaeopumice layer shows concentrated packing of pumice within a relatively uniform sandy matrix (Attenbrow & Hashimoto, in prep.), favouring its accumulation by onshore westerly drift through the oceanic entrance to Port Jackson. Such deposition would precede growth of high dunes on the developing sand barrier. Although it could be driven in by offshore storm activity, the pumice deposit differs from the highly mixed fine and coarse pumice-bearing deposits attributed to episodic tsunamic scouring along the New South Wales coast (Bryant *et al.*, 1992a, 1992b). However, sparse pumice (P4) mixed in later 1800–2800 myr deposits at Balmoral conceivably may be transported by large waves overtopping a higher dune barrier.

Pumice glasses analysed from the main Balmoral layer show some distinct trace element differences between samples recovered from inside the rock shelter (P2) and from outside (P1) the shelter. This could suggest that pumices related to separate eruptions are present in this stratigraphic interval, even though all show a similar olivine-bearing porphyritic dacite character. The dates for these two pumice exposures (3280 ± 60 myrs and 3250 ± 90 myrs) are indistinguishable within error, so this cannot be resolved at this stage. In any event, this pumice layer is intercalated within an aboriginal occupation site which suggests that these peak pumice strandings were witnessed by local inhabitants. Although the precise external source that erupted the main Balmoral pumice influx requires further confirmation, the suggested northern Tonga source would imply a drift of some 4000 km.

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Table 1. Summary of characteristics of pumice from the Balmoral Beach site.

stratigraphic level (age B.P.)	sample numbers	crystals volume	mineral proportions (approx. % by volume)	glass type (%SiO_2)	vesicles % voids
later levels 1800–2800 yrs	P4	3%	Pl(50%),Opx(30%),Cpx(20%) Ol,Ox	rhyodacite (73–74%)	> 60 – < 80%
main level 3300 yrs	P1	5%	Pl(50%),Cpx(20%),Opx(15%) Ox(10%),Ol(<5%)	rhyodacite (72–73%)	> 60 – < 80%
	P2	3–4%	Pl(50%),Opx(30%),Cpx(10%) Ol(<5%),Ox(<5%),Ap	rhyodacite (73%)	> 60 – < 80%
	P5	5%	Pl(55%),Opx(20%),Cpx(20%) Ox(<3%),Ol(<2%),Ap,Zr	rhyodacite (74–75%)	> 60 – < 80%
earlier levels 3300–3500 yrs	P3	2%	Opx(50%),Cpx(40%),Pl(10%) Ox	rhyodacite	> 60 – < 80%
	P6	3%	Pl(50%),Opx(30%),Cpx(10%) Ox(10%)	rhyodacite (75–76%)	> 60 – < 80%
	P7	1%	Qz, Opx, Cpx?, Pl, Ox	rhyodacite (77%)	> 60 – < 80%

Pl, plagioclase feldspar; Opx, orthopyroxene; Cpx, clinopyroxene; Ox, iron oxide; Ol, olivine; Qz, quartz; Ap, apatite; Zr, zircon.

Table 2. Representative analyses, pumice xenocrysts/phenocrysts, Balmoral Beach site.

2A pumice P1 (3,200–3,300 years)

mineral wt%	Ol (1)	Ol (2)	Cpx (c)	Cpx (r)	Opx	Pl (1)	Pl (2)	FeOx (1)	FeOx (2)
SiO_2	40.65	38.71	52.88	52.30	51.34	50.26	56.34	0.09	0.01
TiO_2	0.01	0.05	0.16	0.21	0.17	0.00	0.04	0.00	47.62
Al_2O_3	0.03	0.03	2.28	3.03	0.69	30.60	26.38	0.01	0.19
Cr_2O_3	0.05	0.01	0.14	0.14	0.00	0.00	0.00	0.01	0.00
MgO	49.36	42.85	17.11	16.53	18.43	0.00	0.00	0.00	2.05
CaO	0.27	0.23	23.30	23.08	1.54	14.26	9.80	0.10	0.01
MnO	0.10	0.36	0.15	0.08	1.40	0.00	0.01	0.19	1.06
FeO	9.63	17.32	3.74	4.46	25.59	0.40	0.38	80.82	47.69
NiO	0.21	0.10	0.06	0.00	0.00	0.06	0.02	0.09	0.09
Na_2O	0.03	0.00	0.11	0.14	0.01	3.37	6.01	0.00	0.01
K_2O	0.00	0.00	0.00	0.01	0.00	0.01	0.07	0.00	0.00
total	100.34	99.66	99.93	99.98	99.17	98.96	99.05	81.31	98.73
cations	4[O]	4[O]	6[O]	6[O]	6[O]	32[O]	32[O]	32[O]	6[O]
Si^{4+}	0.994	0.989	1.935	1.916	1.975	9.267	10.238	0.032	0.000
Ti^{4+}	0.000	0.001	0.004	0.006	0.005	0.000	0.006	0.000	1.791
Al^{3+}	0.001	0.001	0.098	0.131	0.031	6.650	5.650	0.004	0.011
Cr^{3+}	0.001	0.000	0.004	0.004	0.000	0.000	0.000	0.003	0.000
Mg^{2+}	1.799	1.632	0.933	0.903	1.058	0.000	0.000	0.000	0.153
Ca^{2+}	0.007	0.006	0.910	0.906	0.064	2.817	1.908	0.038	0.000
Mn^{2+}	0.002	0.008	0.005	0.003	0.046	0.000	0.002	0.057	0.045
Fe^{2+}	0.197	0.370	0.114	0.137	0.824	0.062	0.058	7.912	1.588
Fe^{3+}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	15.929	0.407
Ni^{2+}	0.004	0.002	0.002	0.000	0.000	0.009	0.003	0.025	0.004
Na^{1+}	0.001	0.000	0.008	0.010	0.001	1.205	2.118	0.000	0.001
K^{1+}	0.000	0.000	0.000	0.001	0.000	0.002	0.016	0.000	0.000
sum	3.006	3.009	4.013	4.017	4.004	20.012	19.999	24.000[1]	4.000[1]

Ol(1), olivine(?) xenocryst; Ol(2), olivine phenocryst; Cpx(c), core of zoned phenocryst; Cpx(r), rim of zoned phenocryst; Opx, orthopyroxene phenocryst; Pl(1), plagioclase glomerophenocryst; Pl(2), zoned plagioclase xenocryst; FeOx(1), intersertal iron oxide in plagioclase glomerophenocryst Pl(1); FeOx(2), small euhedral grain.

[1] Fe^{2+} and Fe^{2+} recalculated from total FeO after the method of Droop (1987) and assigned on ideal stoichiometry.

Table 2 (cont.). Representative analyses, pumice xenocrysts/phenocrysts, Balmoral Beach site.

2B pumice P2 (3,200–3,300 years)

mineral wt%	Ol	Cpx (1)	Cpx (2)	Opx (1)	Opx (2)	Pl (c)	Pl (r)	FeOx	FeOx (1)
SiO_2	41.25	52.40	51.02	50.51	51.54	51.51	53.49	0.12	0.02
TiO_2	0.00	0.13	0.25	0.28	0.18	0.02	0.01	14.42	0.83
Al_2O_3	0.04	2.57	0.96	0.82	0.52	30.00	28.75	2.13	0.00
Cr_2O_3	0.00	0.35	0.00	0.03	0.03	0.00	0.00	0.00	0.00
MgO	42.36	16.99	11.74	17.26	18.70	0.00	0.00	1.27	0.00
CaO	0.22	23.09	19.05	1.64	1.54	13.62	12.16	0.01	0.01
MnO	0.25	0.04	0.91	1.48	1.38	0.00	0.04	0.81	0.08
FeO	15.75	3.85	15.31	27.09	25.48	0.45	0.63	75.89	79.89
NiO	0.09	0.02	0.00	0.00	0.08	0.01	0.04	0.01	0.00
Na_2O	0.00	0.11	0.22	0.02	0.02	3.98	4.63	0.00	0.00
K_2O	0.04	0.00	0.00	0.00	0.00	0.02	0.04	0.03	0.00
total	100.00*	99.55	99.46	99.13	99.47	99.61	99.79	94.69	80.83
cations	4[O]	6[O]	6[O]	6[O]	6[O]	32[O]	32[O]	32[O]	32[O]
Si^{+4}	1.035	1.924	1.965	1.964	1.977	9.423	9.728	0.007	0.036
Ti^{4+}	0.000	0.004	0.007	0.008	0.005	0.003	0.001	0.222	3.271
Al^{3+}	0.001	0.111	0.044	0.038	0.024	6.468	6.162	0.000	0.757
Cr^{3+}	0.000	0.010	0.000	0.001	0.001	0.000	0.000	0.000	0.000
Mg^{2+}	1.584	0.930	0.674	1.000	1.070	0.000	0.000	0.000	0.571
Ca^{2+}	0.006	0.908	0.786	0.068	0.063	2.669	2.369	0.004	0.003
Mn^{2+}	0.005	0.001	0.030	0.049	0.045	0.000	0.006	0.024	0.207
Fe^{2+}	0.331	0.118	0.493	0.881	0.818	0.069	0.096	8.201	10.500
Fe^{3+}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	15.542	8.641
Ni^{2+}	0.002	0.001	0.000	0.000	0.003	0.002	0.006	0.000	0.002
Na^{1+}	0.000	0.008	0.016	0.002	0.002	1.412	1.633	0.000	0.000
K^{1+}	0.001	0.000	0.000	0.000	0.000	0.005	0.009	0.000	0.012
sum	2.965	4.015	4.015	4.011	4.008	20.051	20.010	24.000[1]	24.000[1]

Ol, olivine phenocryst; Cpx(1), resorbed clinopyroxene; Cpx(2), clinopyroxene phenocryst in glomeroporphyritic Cpx, Opx, Pl, FeOx cluster; Opx(1), orthopyroxene phenocryst; Opx(2), orthopyroxene phenocryst with Cpx intergrowth; Pl(c), core of zoned plagioclase phenocryst in glomeroporphyritic Cpx, Opx, Pl, FeOx cluster with Cpx(2); Pl(r), rim of zoned plagioclase Pl(c); FeOx, iron-titanium oxide intergrowth with plagioclase glomerophenocrysts; FeOx(l), iron oxide in iron-titanium oxide FeO(x).

[1] Fe^{2+} and Fe^{3+} recalculated from total FeO after the method of Droop (1987) and assigned on ideal stoichiometry.

* normalised analysis.

Table 2 (cont.). Representative analyses, pumice xenocrysts/phenocrysts, Balmoral Beach site.

2C pumice P4 (>1,800–<2,800 years), pumice P5 (3,200–3,300 years)

mineral wt%	Ol (P4)	Cpx (P4)	Opx (P4)	Pl (P4)	FeOx (P4)	Cpx (P5)	Opx (P5)	Pl (P5)	FeOx (P5)
SiO_2	40.68	51.08	51.84	52.29	0.10	52.52	51.10	51.34	0.14
TiO_2	0.00	0.28	0.26	0.04	10.05	0.22	0.20	0.02	14.54
Al_2O_3	0.00	1.33	1.06	29.02	2.24	2.60	0.61	29.93	2.11
Cr_2O_3	0.05	0.00	0.00	0.00	0.07	0.20	0.00	0.00	0.00
MgO	48.75	12.80	20.71	0.00	1.29	16.97	17.99	0.00	1.18
CaO	0.28	19.36	1.48	12.65	0.08	23.49	1.51	13.75	0.00
MnO	0.17	0.57	1.27	0.00	0.39	0.09	1.55	0.00	0.92
FeO	10.71	14.31	23.35	0.43	80.29	3.98	26.67	0.64	77.68
NiO	0.16	0.04	0.00	0.00	0.08	0.13	0.01	0.00	0.00
Na_2O	0.00	0.15	0.00	4.39	0.00	0.17	0.04	3.73	0.00
K_2O	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.03	0.01
total	100.80	99.92	99.97	98.85	94.59	100.27	99.68	99.44	96.58
cations	4[O]	6[O]	6[O]	32[O]	32[O]	6[O]	6[O]	32[O]	32[O]
Si^{+4}	0.995	1.947	1.957	9.606	0.030	1.917	1.969	9.413	0.041
Ti^{4+}	0.000	0.008	0.007	0.006	2.270	0.006	0.006	0.003	3.237
Al^{3+}	0.000	0.060	0.047	6.289	0.793	0.112	0.028	6.468	0.736
Cr^{3+}	0.000	0.000	0.000	0.000	0.017	0.006	0.000	0.000	0.000
Mg^{2+}	1.777	0.728	1.166	0.000	0.578	0.924	1.034	0.000	0.521
Ca^{2+}	0.007	0.791	0.060	2.492	0.026	0.919	0.062	2.701	0.000
Mn^{2+}	0.004	0.018	0.041	0.000	0.099	0.003	0.051	0.000	0.231
Fe^{2+}	0.220	0.456	0.734	0.066	9.578	0.122	0.860	0.098	10.519
Fe^{3+}	0.000	0.000	0.000	0.000	10.590	0.000	0.000	0.000	8.711
Ni^{2+}	0.003	0.001	0.000	0.000	0.019	0.004	0.000	0.000	0.000
Na^{1+}	0.000	0.011	0.000	1.565	0.000	0.012	0.003	1.326	0.000
K^{1+}	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.007	0.004
sum	3.006	4.020	4.012	20.031	24.000[1]	4.025	4.013	20.016[1]	24.000[1]

Ol(P4), olivine phenocryst (part resorbed); Cpx(P4), clinopyroxene phenocryst in Cpx, Opx, Pl, FeOx glomeroporphyritic cluster; Opx(P4), orthopyroxene phenocrysts in Cpx, Opx, Pl, FeOx glomeroporphyritic cluster; Cpx(P5), clinopyroxene phenocryst intergrowth with Ol; Opx(P5), orthopyroxene phenocryst containing apatite, opaque oxides and glass inclusions; Pl(P5), zoned plagioclase phenocryst in Opx, Pl, FeOx and amphibole(?) glomeroporphyritic cluster.

[1] Fe^{2+} and Fe^{3+} recalculated from Total FeO after the method of Droop (1987) and assigned on ideal stoichiometry.

Table 2 (cont.). Representative analyses, pumice xenocrysts/phenocrysts, Balmoral Beach site.

2D pumice P6 (c. 3300 years), pumice P7 (c. 3,500 years)

mineral wt%	Cpx (P6)	Opx (P6)	Pl (P6)	FeOx (P6)	FeS (P6)	Cpx (P7)	Opx (P7)	Pl (P7)	FeOx (P7)
SiO_2	51.26	52.33	46.94	0.06	0.03	51.15	52.20	51.07	0.06
TiO_2	0.28	0.17	0.00	11.10	0.00	0.33	0.06	0.18	10.79
Al_2O_3	1.44	0.94	32.81	2.06	0.01	1.33	29.03	0.60	2.06
Cr_2O_3	0.00	0.01	0.04	0.05	0.00	0.00	0.05	0.00	0.00
MgO	12.90	21.21	0.00	1.09	0.00	13.04	0.00	17.32	1.06
CaO	20.23	1.59	17.30	0.03	0.37	19.60	13.12	1.66	0.03
MnO	0.57	0.89	0.03	0.49	0.04	0.60	0.03	1.00	0.55
FeO	13.05	22.94	0.84	81.20	79.10	13.70	0.57	27.40	79.71
NiO	0.00	0.00	0.03	0.09	0.10	0.00	0.09	0.01	0.04
Na_2O	0.18	0.03	1.84	0.00	0.00	0.16	4.06	0.03	0.00
K_2O	0.02	0.00	0.00	0.03	0.00	0.00	0.05	0.00	0.01
total	99.94	100.11	99.97	96.17	79.57	99.91	99.36	99.27	94.31
cations	6[O]	6[O]	32[O]	32[O]		6[O]	6[O]	32[O]	32[O]
Si^{+4}	1.947	1.964	8.682	0.018		1.946	1.979	9.559	0.018
Ti^{4+}	0.008	0.005	0.000	2.475		0.009	0.005	0.008	2.453
Al^{3+}	0.065	0.042	7.153	0.720		0.060	0.027	6,272	0.734
Cr^{3+}	0.000	0.000	0.006	0.012		0.000	0.000	0.007	0.000
Mg^{2+}	0.730	1.187	0.000	0.482		0.740	1.000	0.000	0.478
Ca^{2+}	0.823	0.064	3.429	0.010		0.799	0.069	2.577	0.010
Mn^{2+}	0.018	0.028	0.005	0.123		0.019	0.033	0.005	0.141
Fe^{2+}	0.415	0.720	0.130	9.857		0.436	0.888	0.087	9.825
Fe^{3+}	0.000	0.000	0.000	10.282		0.000	0.000	0.000	10.327
Ni^{2+}	0.000	0.000	0.005	0.021		0.012	0.000	0.013	0.010
Na^{1+}	0.013	0.002	0.660	0.000		0.000	0.002	1.479	0.000
K^{1+}	0.001	0.000	0.000	0.000		0.000	0.000	0.012	0.004
sum	4.020	4.012	20.070	24.000[1]		4.021	4.003	20.029	24.000[1]

Cpx(P6), clinopyroxene phenocryst with plagioclase inclusions; Opx(P6), orthopyroxene phenocryst with intergrown plagioclase and FeOx; Pl(P6), plagioclase intergrowth with orthopyroxene Opx(P6); FeS, iron sulphide inclusions in Cpx, Opx, Pl glomeroporphyritic cluster; Cpx(P7), clinopyroxene phenocryst; Opx(P7), orthopyroxene phenocryst; Pl(P7), plagioclase phenocryst; FeOx(P7), iron oxide phenocryst intergrowth with Cpx.

[1] Fe^{2+} and Fe^{3+} recalculated from total FeO after the method of Droop (1987) and assigned on ideal stoichiometry.

Table 3. Representative analyses of glass from pumice samples, Balmoral Beach site.

wt%	P1	P2	P2(i)	P4	P5	P5(i)	P6	P7	P7(i)
SiO_2	72.22	72.98	68.94	73.47	74.13	71.40	75.31	76.98	72.51
TiO_2	0.44	0.46	0.52	0.41	0.43	0.41	0.34	0.37	0.36
Al_2O_3	13.19	13.14	13.17	11.61	12.95	12.43	11.19	11.64	11.33
Cr_2O_3	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.00
MgO	0.65	0.57	0.40	0.66	0.51	0.37	0.43	0.47	0.47
CaO	3.49	3.38	3.42	4.14	3.07	2.90	3.08	2.97	3.58
MnO	0.17	0.18	0.13	0.11	0.17	0.25	0.10	0.12	0.12
FeO	3.74	3.47	3.90	4.80	3.72	4.11	3.17	3.31	4.38
NiO	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.02
Na_2O	1.36	1.21	1.10	1.03	1.23	1.36	1.34	1.20	0.94
K_2O	0.70	0.66	0.47	0.79	0.77	0.47	0.90	0.98	0.74
total	95.96	96.05	92.05	97.03	96.98	93.72	95.86	98.06	94.45
CIPW norm (anhydrous norms calculated at $Fe_2O_3/FeO=0.2$)									
qz	53.3	55.7	53.6	56.4	56.2	57.4	58.6	56.6	55.2
or	4.3	4.1	4.8	4.7	3.0	5.6	5.9	4.6	3.0
ab	12.0	10.7	9.0	10.7	12.3	11.8	10.4	8.4	10.1
an	18.0	17.5	21.2	15.7	15.4	15.9	15.0	18.8	18.4
hy	6.3	5.7	7.6	5.8	6.4	5.0	5.1	6.8	5.9
c	4.0	4.5	1.6	4.7	4.7	2.5	3.3	2.6	5.0
mt	1.3	1.2	1.6	1.2	1.4	1.1	1.1	1.5	1.4
il	0.9	0.9	0.8	0.8	0.8	0.7	0.7	0.7	1.1
total	100.1	100.3	100.2	100.0	100.2	100.0	100.1	100.0	100.1
D.I.	69.6	70.4	67.4	71.8	71.4	74.9	74.8	69.7	68.3
An%	60.1	62.1	70.2	59.4	55.6	57.4	59.2	69.1	64.6
Mg No.	27.9	26.8	23.5	23.4	16.7	23.2	24.0	19.3	18.6

P1, 2, 4, 5, 6, 7 groundmass glass; P2(i), P5(i), P7(i) glass inclusions in orthopyroxene; D.I., An% and Mg No. calculations follow procedures in Hughes (1982). D.I., Differentiation Index.

Table 4. Trace element composition (ppm) of representative rhyodacitic glasses and dacite matrix, eastern Australian and Southwest Pacific examples.

locality	Balmoral Beach eastern Australia				Tonga		Kermadec	Lau Basin	
	P2	P4	P6	P7	Metis	Fonualei	Curtis Is	840C-6#	838A-11H
Rb	1.3	15	9.9	274	21	26	6.8	9.2	4.9
Sr	21	232	388	330	130	245	175	98	191
Y	18	27	11	67	25	32	41	21	16
Zr	18	50	20	178	68	61	84	84	49
Nb	0.2	1.0	0.7	11				1.5	0.6
Ba	33	475	643	618	610	380	3.45	153	56
La	0.8	3.0	1.9	45		(4)	4.6	5.8	3.6
Ce	2.5	9.2	4.8	111		(12)	14.4	16.1	8.4
Pr	0.6	1.5	1.1	11					
Nd	3.5	7.1	4.0	42		(9)	11.4	12.1	7.1
Eu	0.3	0.8	0.9	3.3			1.3	1.9	0.8
Sm	1.4	2.8	1.8	8.6			3.6	3.7	2.0
Gd	2.2	2.9	1.9	8.4			5.0		
Ho	0.8	1.6	0.5	1.6					
Yb	2.2	4.0	1.5	6.6			4.0	3.4	
Lu	0.3	0.8	0.3	1.2					
Hf	0.6	2.9	0.7	4.4					
Pb	0.6	8.6	4.7	85			5.1		
Th	0.1	0.6	0.4	22		(0.7)	2.1		
U	0.0	0.9	0.7	8.3		(0.4)	0.8		
La/Yb	0.36	0.75	1.3	6.8			1.15	1.71	0.23
Y/Zr	1.00	0.54	0.55	0.38	0.37	0.52	0.49	0.25	0.33
Rb/Zr	0.07	0.30	0.50	1.54	0.31	0.43	0.08	0.11	0.10
Ba/La	41.3	158	338	13.7		95.0	75.0	26.4	15.6
Sr/Nd	6.0	32.7	97.0	7.86		27.2	15.4	8.10	26.9
Ba/Th	330	792	1608	28.1		543	164		
Ba/Sr	1.57	2.05	1.66	1.87	4.69	1.55	1.97	1.56	0.29
Ba/Rb	25.4	31.7	64.9	2.26	29.0	14.6	50.7	16.6	11.4
Rb/Sr	0.06	0.06	0.03	0.83	0.16	0.11	0.04	0.09	0.03

P2, P4, P6, P7 this work; Metis Shoal and Fonualei, Tonga, from Ewart *et al.* (1973) and Ewart & Hawkesworth (1987); Curtis Island, Kermadec (from Ewart *et al.*, 1977); Lau Basin (from Clift & Vroon, 1996).

Table 5. Mineral and glass compositions and calculated bulk compositions for main layer pumices (P1, P2), Balmoral Beach site.

Pumice P1 (5% xenocrysts/phenocrysts, 20% glass)

	mineral component compositions								glass	bulk
wt%	Plag1	Plag2	Cpx	Opx	Ox1	Ox2	Ol1	Ol2	comp	comp
SiO_2	50.8	56.9	52.6	51.8	0.1	–	38.9	40.5	72.2	67.0
TiO_2	–	–	0.2	0.2	–	47.6	–	–	0.4	0.7
Al_2O_3	30.9	26.7	2.7	0.7	–	0.2	–	–	13.2	13.7
MgO	–	–	16.8	18.6	–	2.0	42.6	49.2	0.7	2.2
CaO	14.4	9.9	23.2	1.6	0.1	–	0.2	0.3	3.5	5.2
MnO	–	–	0.1	1.4	0.2	1.1	0.4	0.1	0.2	0.2
FeO total	0.4	0.4	4.1	25.8	80.8	47.7	–	–	3.7	5.4
Na_2O	3.4	6.1	0.1	–		–	–	–	1.4	1.5
K_2O	–	0.1	–	–		–	–	–	0.7	0.6
% of rock	2.25	0.25	1.0	0.75	0.4	0.1	0.2	0.05	20.0	25.0

Pumice P2 (4% xenocrysts/phenocrysts, 20% glass)

	mineral component compositions						glass	bulk
wt%	Plag	Cpx1	Cpx2	Opx	Ox	Ol	comp	comp
SiO_2	52.7	51.3	52.6	51.8	0.1	41.3	73.0	69.0
TiO_2	–	0.3	0.1	0.2	14.4	–	0.5	0.6
Al_2O_3	29.5	1.0	2.6	0.5	2.2	–	13.1	13.5
MgO	–	11.8	17.1	18.8	1.3	42.4	0.6	2.0
CaO	13.0	19.1	23.2	1.6	–	0.2	3.4	4.3
MnO	–	0.9	–	1.4	0.8	1.2	0.2	0.3
FeO total	0.6	15.4	3.9	25.6	79.9	15.8	3.5	5.3
Na_2O	4.3	0.2	0.1	–	–	–	1.2	1.4
K_2O	–	–	–	–	–	–	0.7	0.6
% of rock	2.0	0.3	0.1	1.2	0.2	0.2	20.2	24.0

Table 6. Comparative bulk and glass compositions, Australia/Southwest Pacific dacites. ND, not determined.

	Balmoral eastern Australia[1]		Metis Shoal Tonga[2]		Herald Cays eastern Australia[3]		Fonualei Tonga[2]	
wt%	(bulk)	(glass)	(bulk)	(glass)	(dark)	(light)	(bulk)	(matrix)
SiO_2	67.0	72.2	63.7	73.6	67.2	73.5	65.6	73.2
TiO_2	0.5	0.4	0.4	0.5	0.6	0.6	0.6	0.4
Al_2O_3	13.7	13.2	12.4	12.3	12.1	11.9	14.0	11.8
Fe_2O_3			1.4	1.3	0.5	0.8	2.1	1.0
FeO	5.4t	3.7t	5.2	2.7	8.5	4.8	6.1	4.3
MnO	0.2	0.2	0.1	0.1	0.1	–	0.2	0.1
MgO	2.2	0.7	5.1	1.1	1.3	0.6	1.4	0.7
CaO	5.2	3.5	7.0	3.6	5.6	3.8	5.7	3.8
Na_2O	1.5	1.4	2.6	3.2	2.6	2.8	3.0	3.2
K_2O	0.6	0.7	0.9	1.5	0.6	0.8	1.1	1.4
P_2O_5	–	–	0.1	0.1	0.2	0.1	0.2	0.2
$H_2O\pm$	ND	ND	0.9	0.1	0.3	0.5	ND	ND
total	96.5	96.0	99.8	100.1	99.6	100.2	100.0	100.0
CIPW anhydrous norms (calculated at Fe_2O_3/Fe_2O_3 + FeO = 0.2); t = total FeO.								
q	40.1	52.9	22.6	38.7	33.3	42.9	27.0	38.6
or	3.7	4.3	5.4	8.9	3.6	4.7	6.5	8.3
ab	13.2	12.3	22.3	27.1	22.2	23.8	25.4	27.1
an	26.8	18.1	19.7	14.8	19.7	17.6	21.5	13.7
di			12.0	2.1	6.0	0.6	4.7	3.3
hy	12.4	6.5	14.9	6.0	11.0	7.3	10.7	6.2
mt	1.8	1.2	2.1	1.3	2.9	1.8	2.6	1.7
il	1.0	0.8	0.8	1.0	1.2	1.1	1.1	0.8
c	1.2	3.9						
ap			0.2	0.2	0.5	0.2	0.5	0.5
D.I.	57.0	69.6	50.3	50.3	59.0	71.4	58.9	73.9
An%	67.0	59.4	47.0	47.0	47.1	42.5	45.8	33.6
Mg No.	47.6	29.7	63.8	63.8	24.5	19.5	28.1	23.1
Na_2O/K_2O	2.5	2.0	2.9	2.1	4.3	3.5	2.7	2.3

[1] from Table 4, this work.

[2] after Ewart *et al.* (1973).

[3] after Bryan (1968).

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Petrographic Temper Provinces of Prehistoric Pottery in Oceania

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ABSTRACT. The mineralogical compositions and petrological character of non-calcareous mineral sand tempers in prehistoric potsherds from Pacific islands are governed by the geographic distribution of geotectonic provinces controlled by patterns of plate tectonics. As sands from different islands are not mingled by sedimentary dispersal systems, each temper sand is a faithful derivative record of parent bedrock exposed on the island of origin. Tempers are dominantly beach and stream sands, but also include dune sand, colluvial debris, reworked volcanic ash, broken rock, and broken pottery (grog). From textural relations with clay pastes, most tempers were manually added to clays collected separately, but naturally tempered clay bodies occur locally. Calcareous temper sands derived from reef detritus are widely distributed, but ancient potters commonly preferred non-calcareous sands for temper. Consequently, beach placer sand tempers rich in diagnostic heavy minerals are typical of many temper suites. Distinctive temper classes include oceanic basalt, andesitic arc, dissected orogen, and tectonic highland tempers characteristic of different geologic settings where contrasting bedrock terranes are exposed. Most Oceanian sherd suites contain exclusively indigenous tempers derived from local island bedrock, but widely distributed occurrences of geologically exotic tempers document limited pottery transfer over varying distances at multiple sites.

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This paper focuses on regional patterns of compositional variation, in terms of mineralogy and petrology, observed for sands contained in prehistoric earthenware pottery of island Oceania. The sands imbedded in the clay bodies are commonly called "temper" because their presence improves the behaviour of the clay during the fabrication of ceramic wares. Conclusions are based on petrographic study, over a span of three decades, of approximately 1200 thin sections made from sherds collected by numerous archaeologists (see acknowledgments) working in island groups of both the southern and western Pacific Ocean (Fig. 1). Although ceramic petrography is notoriously underutilised in archaeology (Schubert, 1986; Stoltman, 1989), it is a powerful tool for the study of Oceanian tempers (Dickinson & Shutler 1968, 1971, 1979). Generically distinctive temper provinces are both theoretically predictable and empirically definable in terms of the sands available to island potters within different geotectonic realms. Indigenous pottery can be identified from the provenance stamp of local island bedrock as reflected in the nature of temper sand grains. Pottery transfer can be detected from the occurrence of exotic

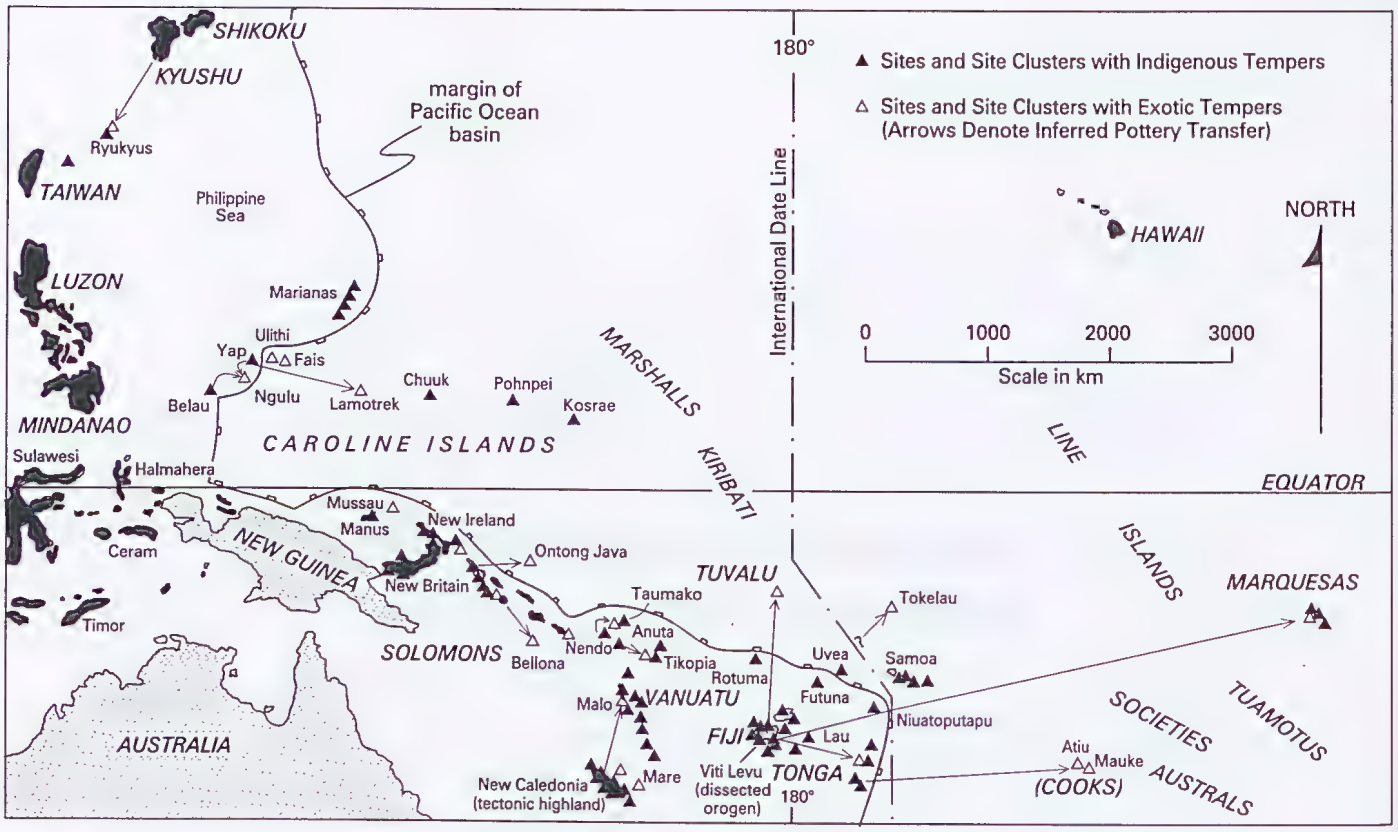

Figure 1. Outline map of island Oceania showing locations of islands and island groups for which temper suites in prehistoric sherds have been studied petrographically. Arrows denote salient prehistoric pottery transfer from sites and site clusters yielding indigenous temper suites (solid triangles) to selected sites yielding exotic temper suites (open triangles).

temper sands that could not have been derived from local island bedrock. Electron microprobe analysis (Freestone, 1982) of selected temper grain types has aided provenance evaluations in selected instances (Dickinson, 1971a; Dickinson *et al.*, 1990).

The success of the regional petrographic reconnaissance reported here stems from the restricted dispersal of sediment in island settings. Each of the small islands within Oceania approximates a point source of local sediment, and sands from different islands never mix, except on the deep sea floor where deposits are inaccessible for collection. Interpretations of sand provenance are consequently less ambiguous than in riverine continental settings, where the mingling of detritus from multiple sources within large drainage basins produces sands of heterogeneous parentage derived from multiple sources (Hays & Hassan, 1974). Elaborate statistical techniques are commonly required to distinguish between temper sands from different continental sites (Mason, 1995), whereas sharp qualitative criteria are typically valid for island settings. This advantage of island sites for temper analysis weakens as the size of islands increases, and the approach used here for island Oceania could not be applied as fruitfully among the larger landmasses of Papua New Guinea, Indonesia, or the Philippines. Other island regions such as the Lesser Antilles are amenable, however, to analogous treatment (Donahue *et al.*, 1990).

The oldest known indigenous pottery in island Oceania dates from 3500–3000 years ago in both the western and southern Pacific regions (Kirch & Weisler, 1994; Rainbird, 1994). In places where earthenware pottery is still made within Oceania, modern products are technologically similar to prehistoric wares, although vessel shapes and decorative styles have varied geographically and through time. Studies of both temporal and areal typology provide a rich context of archaeological interpretation, much of it still incomplete, that is beyond the scope of this paper on the geographic distribution of different temper suites regardless of the ages of the sherds examined. At typical sites, indigenous sherds of varied ages contain similar tempers representing sands that were locally available to resident potters throughout extended intervals of prehistoric time (Dickinson, 1973, 1976; Dye & Dickinson, 1996; Dickinson *et al.*, 1996).

Temper terminology

People who make earthenware pottery need to insure that clay bodies contain an adequate proportion of gritty non-clay constituents, both to enhance workability before firing and to impart strength and durability to fabricated ceramic pieces during and after firing. To achieve the desired consistency, some selected non-clay

aggregate, typically sand, is commonly kneaded by potters into wetted clay prior to the shaping and firing of ceramic wares. This manufacturing technique is commonly described as tempering the clay. In prehistoric potsherds, however, the distinction between manually added grains and analogous grains that may have been imbedded naturally in clay bodies must be derived from inferences based on textural criteria.

Appropriate descriptive terminology is not straightforward for the coarser grained, rigid components of earthenware that are not deformed as the surrounding clay is worked. Although long called "temper", such materials have also been termed "nonplastic inclusions" (Shepard, 1965; Rice, 1987), a usage chosen to avoid any connotation of deliberate addition to clay bodies and thus to allow for cases where sufficient aplastic material was imbedded within clays as initially collected. To describe separate grains as "inclusions" is awkward, however, because in mineralogical tradition the word "inclusion" denotes a crystal or crystal cluster wholly enclosed within an individual crystal of another mineral. The usage of "temper" as a non-generic term can be preserved, without turning to the petrographically ambiguous word "inclusion", if "natural temper" is contrasted with manually added temper in cases where the generic distinction can be made.

In general, however, grains of both natural and manually added temper sand may well occur jointly in some earthenware made from sandy clay bodies containing less than the optimal proportion of sand without further manual addition of temper. One may even speculate that sand-poor and "naturally tempered" sand-rich clays could have been mixed together in some instances to achieve the desired proportion of temper. In prehistoric Oceania, however, textural relations between temper sands and surrounding clay pastes in most of the sherds examined for this study show that the typical procedure of island potters, in parallel with the practice of modern studio potters, was to add separately collected temper sands to fine-textured clays lacking, in their natural state, any appreciable fraction of sand.

Temper-paste relations

Clay bodies used for prehistoric ceramic manufacture on Pacific islands were doubtless collected variously from soils, floodplains, and possibly tidal flats. The clay pastes of typical sherds are silty to varying degrees, although grains smaller in diameter than the thickness of a standard thin section (0.03 mm) cannot be discerned individually by optical petrographic methods. In the dominant sherds studied from almost all locales, roughly a quarter to a third of the volume of each sherd is composed of temper sand that forms a distinctly coarser grain population than the silty clay of the paste in which the sand grains are imbedded. Temper grains range in different instances from 0.1 to 1.0 mm in mean diameter, with finer or coarser sand used in irregular patterns throughout the Oceanian region.

The characteristic contrast in grain size between paste and temper implies manual addition of sand to clay by the ancient potters, although sparingly observed gradations in grain size between paste and temper suggest naturally tempered colluvial or alluvial clay bodies in selected instances. Presumed distinctions between natural and manually added temper may be moot if potters exploited some fluvial deposits where alternating clay-rich and sand-rich laminae could be collected jointly and then kneaded together to form mixed material of the appropriate texture and consistency.

Temper textures

As expected from the coastal settings of many island archaeological sites, well sorted beach sands composed of rounded to subrounded grains are the most widespread Oceanian tempers, but only moderately sorted aggregates composed of subangular to subrounded grains and interpreted as stream sands are also common, except in island groups lacking surface drainages. The choice of stream sands for temper on islands with few large drainages may stem partly from the convenience of collecting stream sand near pits dug into floodplains or stream banks to collect clay bodies. Admixtures of calcareous grains derived from offshore fringing or barrier reefs are common in many beach sands, and serve as one signal of coastal origin, but reworked carbonate grains ("limeclasts") derived from erosion of uplifted reef complexes also occur in some stream sands.

Less common Oceanian tempers include poorly sorted aggregates of weathered particles with irregular shapes derived from winnowed slopewash colluvium, well sorted littoral dune sands, slightly reworked volcanic ash, and jagged fragments of volcanic rock perhaps derived from wastage in adze quarries. Rarely, the only temper present in some sherd assemblages is "grog", composed of fragments of previously fired pottery which can be identified only with difficulty in thin section as inhomogeneities within clay pastes (Whitbread, 1986). Grog fragments appear as isolated domains of irregular angular shape having a different texture or fabric than the surrounding clay body. Grog temper is dominant in sherds from Palau, common in sherds from Yap, and present in selected sherds from the famed Nan Madol site on Pohnpei in the central Caroline Islands, and from Ofu in American Samoa (Dickinson, 1993). Grog temper was presumably used where nearby deposits of sand suitable for temper were not readily available, although cultural tradition may well have played a role in the choice of grog for temper.

Calcareous tempers

Locally throughout Oceania, some sherd assemblages or sub-assemblages contain beach sand tempers composed exclusively or dominantly of calcareous reef detritus. The provenance of the calcareous grains is indeterminate on petrographic grounds because reef characteristics are

similar throughout the region. Fortunately for a regional reconnaissance of temper compositions, many ancient potters apparently preferred to use non-calcareous sands as temper, even at sites where nearby white-sand beaches of reef debris are the most abundant readily available source of potential temper sand. The preferential selection of non-calcareous black sand for temper probably stemmed from the tendency for calcareous grains to disintegrate from calcining, which causes spalling of pots within the temperature range achieved by firing earthenware in open bonfires where close control of temperature is not feasible (Rye, 1976; Bronitsky & Hamer, 1986; Intoh, 1990; Hoard *et al.*, 1995).

Placer tempers

Avoidance of calcareous sand was achieved in different instances by seeking black-sand beaches or stream deposits of bedrock detritus, or by collecting placer concentrates of black mineral sand on beaches composed of mixed calcareous and non-calcareous sand (Dickinson, 1994). The use of beach placer concentrates for temper sand, as in Tonga (Dye & Dickinson, 1996; Dickinson *et al.*, 1996), is sure evidence that non-calcareous sand was preferred as temper, for its collection required deliberate avoidance of more abundant associated calcareous sand at some inconvenience to the collectors. The use of placer concentrates, whether collected from beaches or streambeds, may also have served in many places to reduce the proportion of glass-rich volcanic rock fragments in temper. Placer sands are enriched in dense minerals of high specific gravity with respect to polyminerallic rock fragments as well as with respect to calcareous grains, and hydrated volcanic glass in the groundmasses of volcanic rock fragments could also be unstable in earthenware if firing promoted dehydration of the glass.

The common occurrence of placer mineral aggregates in Oceanian sherds provides a fortuitous advantage for provenance interpretations, because dense ferromagnesian silicate minerals of high specific gravity are commonly the most diagnostic components of bedrock assemblages, even where present in only accessory or varietal abundances in the source rocks. For studies of sediment provenance, petrographers often separate heavy minerals artificially, using flotation in heavy liquids, from the other, more abundant sand grains present in a given detrital aggregate. The ancient potters of Oceania, for reasons of their own, often achieved an analogous concentration of heavy minerals through their temper-collecting habits. The knowledge that Oceanian sherd tempers reflect various restrictive collections of available sands means, however, that the sherd tempers do not represent statistically valid samples of the full range of local island sands.

Temper-clay sources

The question of how closely temper sands in Oceanian sherds relate to the clay bodies in which they are imbedded is a vexed one. In the case of natural tempers, the source of the sand and the clay is identical, but the conclusion that a given temper was not manually added is always interpretive in hindsight. In the prevalent cases where textural evidence for manual addition of sand temper is strong, the sources of sand and clay were clearly not identical. For inferences about temper sources, it is immaterial whether natural or manually added temper is involved, except that petrography alone cannot address the question of how far sand or clay may have been transported before the two were mixed together by ancient potters. For detailed provenance studies beyond the scope of this review, it is also useful to distinguish between non-local temper that may nevertheless have been derived from some other part of the same island where the sherds containing it were recovered, and truly exotic temper that is indicative of derivation from a different island or island group.

It seems likely in most cases that the presence of distinctly non-local or exotic temper in sherds from a given site reflects pottery transfer after manufacture, rather than movement of sand as raw material before firing. Given the technological constraints of ancient island cultures, the transport of bulk raw materials for long distances, either on foot or by canoe, would have presented severe challenges, and few sites are located where no sands at all are available nearby. On the other hand, the desire for some special kind of temper, such as placer sand, may have been strong in some instances, and temper is both less fragile and less bulky than finished wares, as well as representing only a fraction of the overall weight of ceramic wares. In general, it is well to bear in mind that petrography alone cannot distinguish between transport of temper and transport of finished wares.

The sourcing of clay bodies in prehistoric sherds presents a different and more difficult problem than the sourcing of sand tempers, and petrographic methods are ineffective because of the submicroscopic grain size of clay particles. Beyond that technical consideration, sand grains are largely unmodified pieces of parent bedrock and carry a clearcut provenance signal, whereas clays are produced by wholesale mineralogical modification of bedrock by weathering (Garrels & Mackenzie, 1971: 142–170). The mineralogy of clays, whether residual in soil or transported and redeposited as alluvium, reflects the local geochemical environment of a weathering horizon, and may be as dependent upon the local climate or microclimate as upon the nature of the parent bedrock (Blatt *et al.*, 1980: 272–273; Blatt, 1982: 42–44). For example, alumino-silicates of the kaolin group, which lack metallic elements other than Al and Si in their crystal lattices, form only where oxidation of iron to the ferric state is strong and rainfall is sufficient for percolation to leach alkalis (Na, K), alkaline earths (Ca, Mg), and appreciable silica (Si) downward from the soil horizon, whereas formation of the smectite group of more complex chemistry requires retention of silica and some combination of alkaline earths (Ca, Mg), alkali metal (Na), and ferrous iron within the soil horizon owing to ineffective leaching, whether from inadequate moisture or poor infiltration that leads to water logging of surficial

layers (Keller, 1970). Clays of varied mineralogy and geochemistry can thus form from the same bedrock in different geomorphic settings, whereas quite similar clays can form in similar geographic settings from a rather wide range of parent bedrock types.

Chemical analysis of clay bodies can be employed in attempts to match sherd pastes with specific potential clay sources, but in general is not an attractive tool for regional reconnaissance of sources for raw materials in the way that temper sands can be studied petrographically for comparison with what is known of potential bedrock sources. For clay analysis, moreover, care must be taken to allow for the effect of associated temper on the bulk chemical compositions of sherds (Schubert, 1986; Neff *et al.*, 1989; Arnold *et al.*, 1991; Ambrose, 1992, 1993). Microprobe analysis of clay paste apart from temper grains is the most direct means to avoid contaminating results from clay analysis with the chemistry of manually added tempers (Summerhayes, 1997).

Geotectonic realms

The generic mineralogical and petrological character of island sands is governed by the irregular distribution of key Pacific geotectonic realms (Fig. 1). The overall geography of different temper provinces is dictated by the pattern of movement of major plates of lithosphere in the geometric dance of plate tectonics (e.g., Oxburgh, 1974; Kearey & Vine, 1990). The Pacific plate of lithosphere including most of the islands of Polynesia and Micronesia is moving toward the northwest, relative to Asia and Australia, and descends beneath the edges of the Eurasian and Indo-Australian plates along subduction zones marked by the deep trenches of the western and southwestern Pacific. Isolated archipelagoes and linear island chains of the Pacific plate were built exclusively by intraoceanic volcanism above hotspots in the underlying mantle, whereas linear and curvilinear island chains along the edges of the adjacent Eurasian and Indo-Australian plates were built by arc magmatism and tectonism influenced by the descent of lithosphere into the mantle beneath the island arcs.

The overall picture is complicated by the existence of island arcs of reversed polarity in Melanesia, where current subduction beneath New Britain, the Solomon Islands, and Vanuatu is downward to the northeast, involving oceanic lithosphere of marginal seas lying to the east of Australia and New Guinea, rather than the Pacific plate (Kroenke, 1984). In the Ryukyu Islands, subduction of normal polarity, downward away from the Pacific basin, nevertheless involves marginal-basin lithosphere of the Philippine Sea (Seno & Maruyama, 1984). Even island arcs of normal polarity in Tonga and the Mariana Islands are backed by marginal seas of oceanic character, and in that sense are interoceanic, as contrasted with arcs such as the Andes or Sunda (Sumatra-Java) built along the edges of continental blocks (Dickinson, 1975).

The petrology and consequent mineralogy of intraoceanic and island-arc igneous assemblages are fundamentally different because intraoceanic volcanism is triggered by simple decompression melting of advecting mantle (Jarrard & Clague, 1977), whereas arc magmatism involves more complex processes related to subduction of lithosphere (Anderson *et al.*, 1978). The salient additional factor is probably the release of volatiles, chiefly water, from subducting slabs of lithosphere as they warm during descent into the mantle. The rising volatiles can flux the overlying mantle wedge to produce types of melts unknown from intraoceanic settings, including hydrous magmas capable of generating the explosive eruptions so common along island arcs.

As island arcs evolve above subducting slabs, large bodies of derivative magma are also commonly trapped within island arc crust to form intrusive bodies, including granitic plutons, of a size and composition unlike the subvolcanic dikes and sills of limited volume known from intraoceanic settings (Dickinson, 1970). Along the flanks of island arcs, moreover, the structural effects of subduction include the detachment of seafloor sediment from the surfaces of descending slabs of oceanic lithosphere, and their tectonic stacking into folded and thrust-faulted piles of deformed strata termed subduction complexes (Dickinson, 1972). The subduction complexes in some cases contain fault-bounded slivers of oceanic lithosphere, composed of both crust and mantle horizons jointly termed an ophiolite succession (Moores, 1982), and can be driven beneath analogous ophiolite slabs underpinning interoceanic island arc structures composed of arc igneous assemblages.

Temper classes

Geotectonic relations thus dictate that Oceanian temper suites fall into four broad classes distinguishable on qualitative grounds despite large quantitative variations in temper composition within each class: (*a*) *oceanic basalt* tempers in clusters and chains of shield volcanoes built by hotspot volcanism piercing the oceanic plate; (*b*) *andesitic arc* tempers of undissected, though either active or dormant, magmatic arcs fostered by subduction of oceanic lithosphere; (*c*) *dissected orogen* tempers occurring where deep erosion has bitten into the plutonic roots of magmatic arcs; and (*d*) *tectonic highland* tempers where seafloor lavas and sediments overlying ultramafic mantle lithosphere have been uplifted by folding and thrust faulting associated with subduction. Oceanic basalt and andesitic arc tempers include exclusively volcanic detritus, augmented locally by minor contributions from injected dikes and sills, but the dissected orogen and tectonic highland classes include detritus in locally varying proportions from plutonic, metamorphic, and sedimentary rocks as well. Preliminary appraisals of the four temper classes by Dickinson & Shutler (1968, 1971, 1979) are here sharpened and augmented through results and insights from petrographic observations over the past two decades involving sherds from many localities not included in previous analyses.

The designations adopted here for the four generic temper classes should be regarded as convenient labels, rather than as complete descriptions. For example, oceanic basalt tempers, in the usage intended here, include tempers derived from trachyte and other differentiates of intraoceanic basalt magmas, and andesitic arc tempers include tempers composed of basaltic or dacitic debris from the igneous assemblages of island arcs. A brief discussion of each geotectonically defined temper class serves to clarify these and related points. As variable amounts of opaque iron oxide grains (magnetite or ilmenite or both) are present in most tempers, only the non-opaque grain types are discussed in detail.

Oceanic basalt tempers

Oceanic basalt tempers occur in sherds from (*a*) Chuuk, Pohnpei, and Kosrae in the Caroline Islands; (*b*) Rotuma and Uvea in the northern Melanesian borderland; (*c*) Upolu, Tutuila, and Ofu in Samoa; and (*d*) Hiva Oa, Nuku Hiva, and Ua Huka in the Marquesas Islands. The only grain types are volcanic rock fragments of variable texture and phenocrystic minerals of sand size. Individual temper types vary widely in texture, depending upon the sedimentological nature of the aggregate used as temper, and also vary mineralogically, both in ways that reflect strictly local variations in parent bedrock and in ways that reflect more systematic empirical variations in the volcanic assemblages of different island groups. Rounded beach sands are most common but reworked ash and colluvial debris was also used for temper locally. Homogeneous aggregates of angular sand, evidently produced by crushing volcanic rock, were used locally as temper on both Upolu and Tutuila in Samoa, and may represent wastage from adze quarries.

Typical volcanic rock fragments are mafic lava, dominantly olivine basalt or hawaiite but locally including more silica-undersaturated (feldspathoid-bearing) basanite or tephrite, with intergranular to intersertal internal textures displaying twinned plagioclase laths associated with tiny crystals of clinopyroxene and olivine. Minor proportions of coarser grained microgranular dike rocks (dolerite or diabase) are also present in some tempers. Other rock fragments, dominant in some temper types, include hydrated basaltic glass (palagonite), vitrophyric grains with glassy groundmasses in which tiny plagioclase microlites are set, and felsic basaltic differentiates such as trachyte and mugearite in which plagioclase or anorthoclase feldspar is typically the most abundant groundmass mineral.

Mineral grains are dominantly olivine, clinopyroxene, and plagioclase, although hornblende occurs locally in trachytic tempers, known to date only from Samoa. Quartz is characteristically absent, although minor amounts of quartz might well appear in tempers that could potentially be derived from locally exposed quartz-bearing trachytes. The ratio of olivine to clinopyroxene is consistently higher than in andesitic arc tempers (see below), reflecting the generally alkalic character of intraoceanic basalt magmas throughout the western and southern Pacific regions. In Hawaii, subalkalic tholeiitic basalts, which are less undersaturated with respect to silica, are the dominant shield-building lavas, with alkalic magmas erupted only late in the volcanic history of each island. Tholeiitic basalts are unknown, however, among the archipelagoes that have yielded prehistoric pottery.

Andesitic arc tempers

Andesitic arc tempers occur in sherds from (*a*) Guam, Rota, Tinian, and Saipan in the Mariana Islands; (*b*) Belau in the Caroline Islands; (*c*) Manus, New Britain and New Ireland in the Bismarck Archipelago; (*d*) Bougainville, the Shortland Islands, the Santa Cruz Islands, the Duff Islands, Vanikolo, Anuta, and Tikopia in the Solomon Islands; (*e*) the Torres and Banks Islands, Santo, Malo, Malakula, Efate, Erromango, Tanna, and the Shepherd Islands in Vanuatu; (*f*) Futuna and Alofi in the Horne Islands of the northern Melanesian borderland; (*g*) the Yasawa Islands, Kadavu and the Lau Group of Fiji; and (*h*) Niuatoputapu, Vavau, the Haapai Group, and Tongatapu in Tonga. As for oceanic basalt tempers, the only grain types are volcanic rock fragments, including minor dike rocks, and phenocrystic minerals, but the variety of rock fragments and mineral grains is much greater regionally, and locally as well in many instances. Regional variations in the petrologic character of different island arcs is reflected by systematic variations in the mineralogy of derivative temper sands (see section below on temper compositions). Based upon textural criteria, the use of stream sands for temper was as widespread as the use of beach sands along the island arcs of rugged relief.

Typical rock fragments are andesite or basaltic andesite with groundmasses of hyalopilitic to pilotaxitic texture dominated by tiny untwinned plagioclase microlites. Microporphyritic grains, including glassy vitrophyric varieties, some with semiopaque tachylitic groundmasses, are common in many tempers. The variety of volcanic rock fragments is great, however, reflecting the large range of rock types, from basalt to dacite, common along many island arcs. Empirical variations in the textures and compositions of dominant rock fragments provide useful criteria for distinguishing between tempers from different islands in many instances. Microscopic distinctions between andesitic and dacitic rock fragments are inherently intractable, however, unless quartz microphenocrysts are present as an indicator of dacite or rhyodacite.The associated basalts are subalkalic island-arc tholeiites, and contain distinctly less olivine than intraoceanic alkalic basalts and basanites.

Mineral grains are characteristically plagioclase and clinopyroxene or hornblende, or both, but proportions vary widely, and subordinate grains include orthopyroxene, oxyhornblende, and olivine, with variable but typically minor amounts of quartz also present in some tempers. Systematic variations in the content of different ferromagnesian minerals provide multiple criteria for

distinguishing between the tempers of different islands and island groups (see section below on temper compositions).

An unusual island-arc temper rich in rock fragments of metagabbro occurs in sherds from Eua, lying along the front of the Tongan arc where uplift has evidently exposed the ophiolite underpinnings of the arc structure. The rifting of arc structures to form marginal seas can also give rise to volcanic suites indistinguishable from intraoceanic shields. That unusual geotectonic setting is apparently responsible for the presence of oceanic basalt temper at Rotuma, and similar oceanic basalt temper might be characteristic also of Niuafoou, which rises from the floor of the oceanic Lau Basin west of the Tongan arc.

Dissected orogen tempers

Dissected orogen tempers occur in sherd suites studied to date from parts of the Ryukyu Islands and along the southern and western coasts of Viti Levu in Fiji, but could also occur in sherds that might be found in the future on the larger and more geologically varied islands of the Solomons chain, such as Guadalcanal. Grain types reflect derivation from a wide variety of arc volcanic rocks, granitic to dioritic plutons, and both metavolcanic and metasedimentary wallrocks of the plutons. Polyminerallic rock fragments include microgranular plutonic and hornfelsic varieties, as well as a range of microlitic to felsitic volcanic-metavolcanic rocks and metasedimentary argillite-slate-phyllite. Mineral grains include abundant quartz and both feldspars (plagioclase, often altered to albite, and K-feldspar), and less abundant ferromagnesian minerals including biotite, hornblende, and clinopyroxene in varying proportions. Along the northern coast of Viti Levu, and on nearby islands of the Fiji platform (Taveuni and Lomaiviti), volcanic sand tempers derived from post-orogenic cover rocks resemble the more basalt-rich tempers of undissected andesitic island arcs.

Tectonic highland tempers

Tectonic highland tempers occur in sherd suites studied to date from Yap and New Caledonia, but might also occur in islands along the eastern fringe of the Solomons chain where uplifted segments of the intraoceanic Ontong Java Plateau have been incorporated tectonically into the flank of the island arc. There are two contrasting subclasses of tectonic highland temper: (*a*) metasedimentary detritus rich in quartz, quartzite, chert, and foliated tectonite (slate-phyllite-schist) grains; and (*b*) ophiolitic detritus rich in basalt-metabasalt, serpentinite, and pyroxene grains. Blueschist-facies minerals, such as the amphibole glaucophane, restricted to subduction complexes metamorphosed at high pressure but low temperature, occur in accessory amounts in some temper types from New Caledonia.

Grain counting

To compare tempers of different compositions in more than a qualitative anecdotal fashion, some reproducible measure allowing quantitative representation is needed. For modal analysis of sandstones, sedimentary petrologists use the point-counting method (Chayes, 1956), whereby the grains beneath the intersection points of an equidimensional rectilinear grid superimposed on a thin section are identified and counted, with counts summed to determine overall percentages of different grain types. In practice, the grid is generated by moving the microscope stage in fixed increments, along parallel paths spaced the same fixed distance apart, to place different grains beneath the crosshairs. Point-counting provides a reliable estimate of the true volumetric proportions of different grain types, but is time-consuming and the majority of points for thin sections of potsherds always fall within clay paste, yielding no information about tempers. As there is no systematic statistical relationship between the volumetric proportions of different types of temper grains and their counterparts in parent source rocks, there is no inherent advantage to point-counting sherds that compensates for the excessive time required. Although knowledge of the proportions of clay paste in sherd suites is useful for analyses of ceramic technology, the lack of any systematic regional variations in the respective percentages of clay paste and temper in Oceanian sherd suites means that ratios of temper to paste provide no reliable information about the provenance of temper sands.

For quantitative temper study, less time-consuming counts of grain frequency are accordingly adopted here as the basis for compositional comparisons. In practice, different types of temper grains are counted as the microscope stage is traversed across a thin section and grains pass in succession through the field of view. Percentages of grain types are then calculated by summation. As any count represents only a statistical sampling of the total population of temper grains within a sherd, the counting error (one standard deviation) is given by the square root of $p(100-p)/n$ where p is the percentage of a given grain type as estimated from a frequency count and n is the total number of grains counted (Plas & Tobi, 1965). Fully adequate precision is attained by counting 400 grains, although fewer than this target number may be present in standard thin sections of some sherds containing sparse or coarse temper. Depending on the size of each sherd and the nature of its temper, all temper grains present in the thin section may be counted, or only those grains present within selected bands of appropriate width and spacing across the sherd or within equally sized fields of view spaced evenly within the sherd. The method can be viewed as a blend of area-counting and ribbon-counting, which yield essentially identical frequency values (Middleton *et al.*, 1985). Although frequency counts do not yield the same percentage values as point counts (Dye & Dickinson, 1996), they are equally reproducible and thus equally satisfactory for comparative purposes.

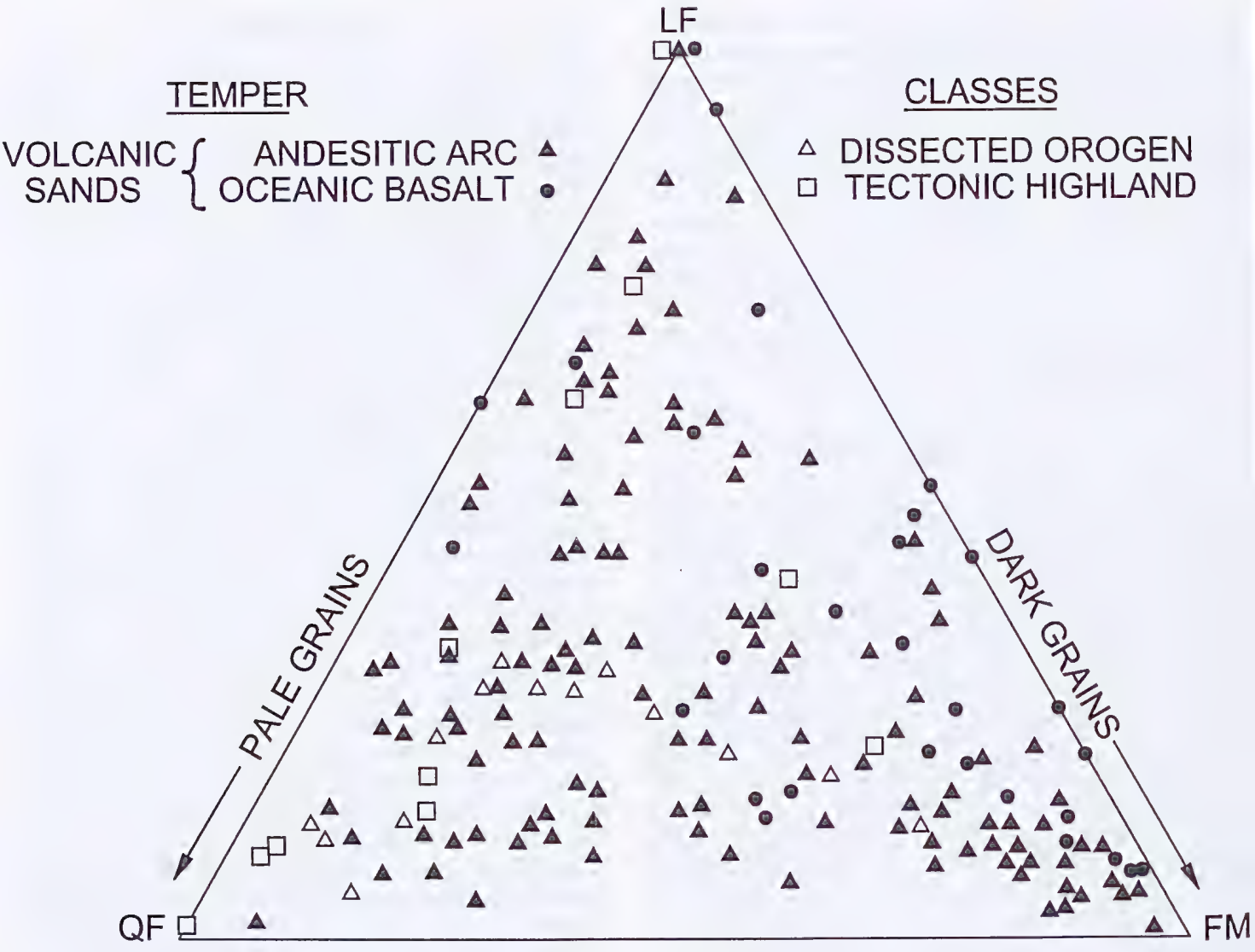

Figure 2. Compositions of Pacific island temper sands in LF-QF-FM space (quantitative triangular diagram) where LF = polycrystalline-polyminerallic lithic fragments (typically shades of grey), QF = quartz and feldspar mineral grains (pale or translucent), FM = ferromagnesian silicate and oxide mineral grains (black or dark green). Plotted points are average compositions of temper types at multiple sites (Fig. 1), but some local temper suites include multiple temper types plotted separately.

Temper compositions

Raw counts may incorporate as many different grain types as desired, based upon mineralogy, internal fabric, and colouration. For the regional comparisons drawn here, grain types are grouped into generic categories to allow depiction of mean temper compositions on triangular plots that represent quantitative graphs of grain frequencies. In tempers that contain non-diagnostic calcareous grains, grain frequencies have been recalculated to 100%, free of calcareous grains. The full non-calcareous grain populations of all studied Oceanian temper types are shown on the LF-QF-FM plot (Fig. 2), which indicates that little or no discrimination between different classes of Oceanian temper is achieved by such simple recalculation of the raw data. This means that even careful megascopic observation of pale grains (QF), greyish grains (LF), and dark grains (FM) in Oceanian tempers has limited scope for provenance determination. The fundamental reason for the failure of the LF-QF-FM plot to display temper contrasts is the fact that generically related placer and non-placer sand aggregates plot very differently in LF-QF-FM space.

Placer concentration of heavy ferromagnesian mineral grains of high specific gravity moves plotted points for closely related temper types systematically toward the FM pole (Fig. 3). Analogous placer effects are shown by the QF-FS-OO plot (Fig. 4), representing the population of monominerallic mineral grains from which polyminerallic lithic fragments have been excluded (FS + OO = FM). Trends of variation between generically related temper types on this plot trend away from the QF pole for low-density quartz and feldspar grains toward the bottom leg of the triangle connecting the FS pole for ferromagnesian silicates to the OO pole for opaque iron oxides. In several instances, an initial placer concentration of mainly ferromagnesian silicates (FS) is succeeded by further placer concentration of rarer opaque iron oxides (OO) because

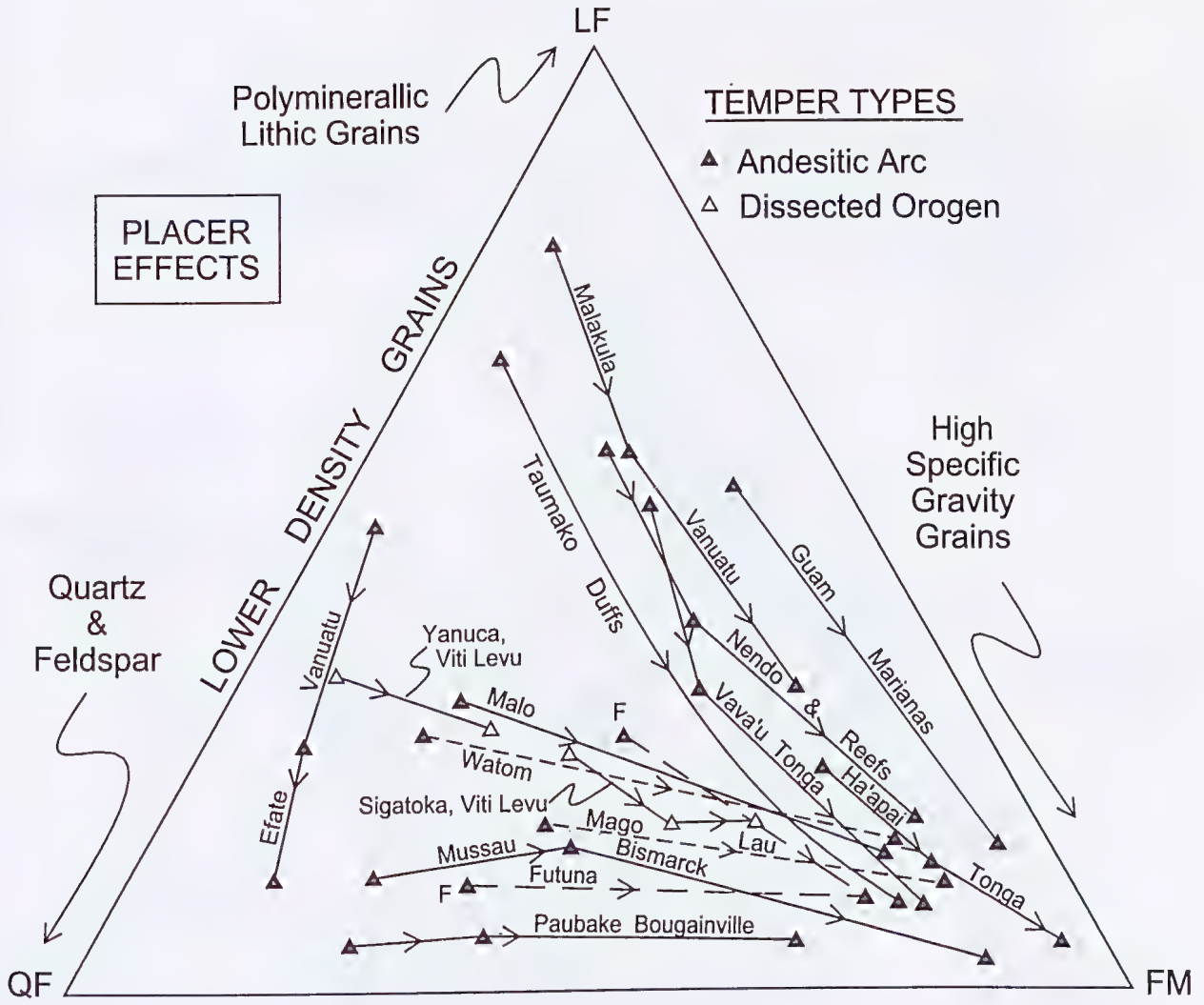

Figure 3. LF-QF-FM plot (see Fig. 2 for poles) showing the effects of fluvial-beach-dune placering (hydraulic concentration of FM grains with higher specific gravity) on temper sand compositions. Plotted points are average compositions of individual temper types, including non-placer and placer aggregates, which form generically related variants of local temper suites and are connected by arrows showing compositional trends governed by progressive placer concentration (in some cases, transitional or intermediate variants are plotted along trends between non-placer and placer end members of temper suites). The seemingly anomalous trend of the Efate temper suite in Vanuatu reflects placer concentration of quartz and feldspar mineral grains (QF) by hydraulic separation from less dense lithic fragments (LF) that are dominantly pumiceous volcanic glass of low specific gravity.

the oxides have inherently greater density than the silicates.

More selective plots reveal differences between Oceanian temper classes more clearly. The Q-F-LF plot (Fig. 5) of quartz and feldspar plus polymineralic lithic fragments, with all ferromagnesian grains excluded, successfully achieves separation of dissected orogen and tectonic highland tempers from each other and from undifferentiated volcanic sand tempers of both the oceanic basalt and andesitic arc classes. The general paucity of quartz grains in all volcanic sand tempers of Oceania is well displayed on this plot. The Q-F-FS plot (Fig. 6) of quartz and feldspar plus ferromagnesian silicate mineral grains (non-opaque FM), with both polymineralic lithic fragments and opaque grains excluded, achieves an analogous separation.

Plotting the FS population of non-opaque ferromagnesian silicate grains for volcanic sand tempers separately, on the hornblende-pyroxene-olivine graph (Fig. 7), brings oceanic basalt and andesitic arc temper types into different compositional fields, with the abundance of olivine in oceanic basalt tempers as the key discriminant. This plot also shows that different island arcs can be discriminated on the basis of hornblende-to- pyroxene ratio. Relatively primitive island arcs, such as Tonga and the Mariana Islands, have eruptive suites dominated by pyroxene andesites and associated island-arc tholeiites, whereas more evolved arcs, such as Vanuatu and the Solomon Islands, also erupt significant quantities of hornblende-bearing lavas. On strictly empirical grounds, a consistent distinction also emerges on the basis of

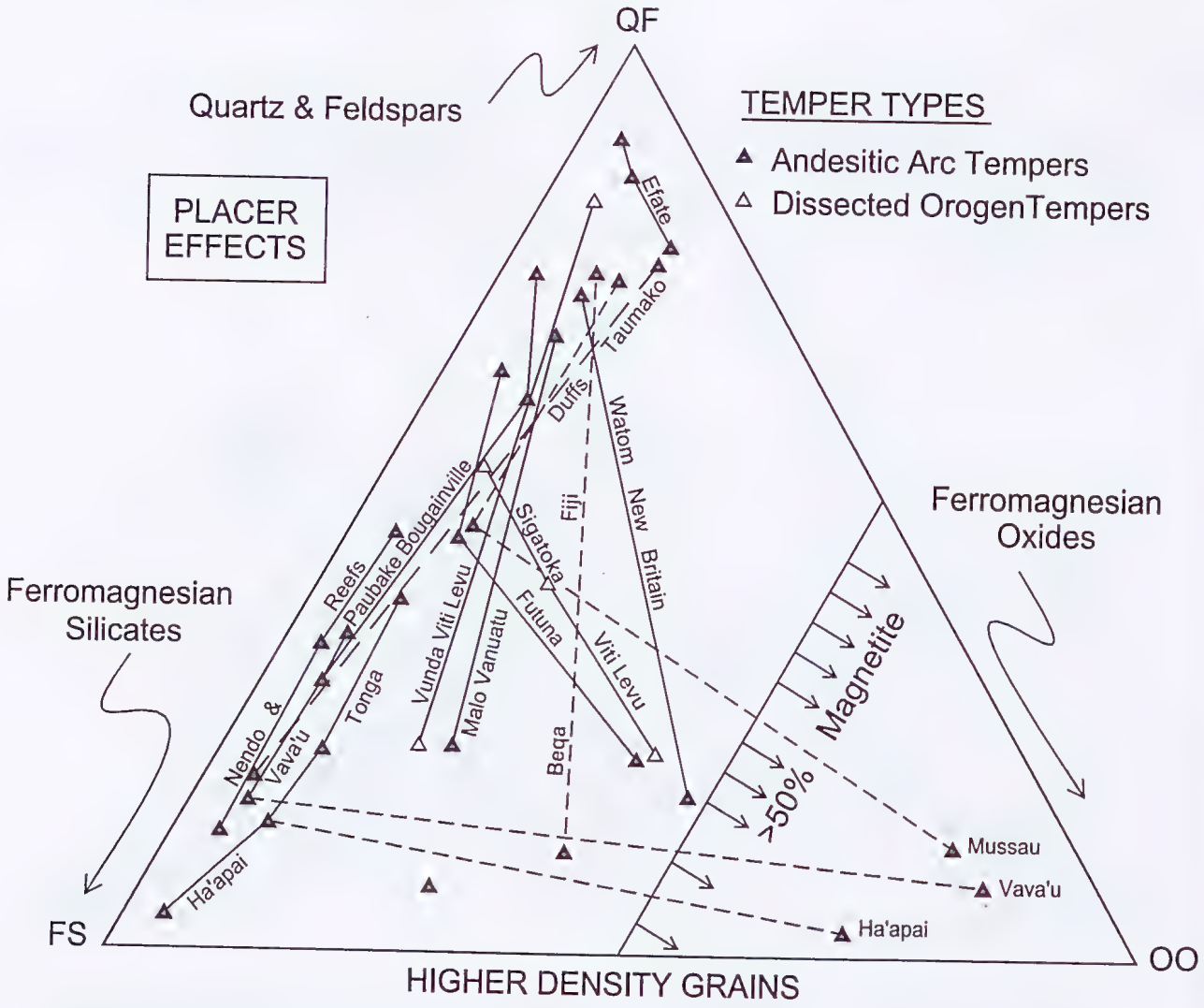

Figure 4. Placering effects (see Fig. 3) on temper sand compositions as displayed on a triangular plot of the QF-FS-OO population, representing mineral grains only (proportions recalculated exclusive of polycrystalline-polymineralic lithic fragments), where QF = quartz and feldspar, FS = ferromagnesian silicates (clinopyroxene, orthopyroxene, hornblende, oxyhornblende, olivine, biotite, epidote), and OO = opaque iron oxide grains (dominantly magnetite but also including maghemite, ilmenite, hematite, chromite in some cases). Placer concentration proceeds downward from the QF pole (grains of lowest specific gravity) along trends defined by lines connecting non-placer and placer variants of local temper suites, and in some cases pursues further trends toward the OO pole (grains of highest specific gravity).

hornblende-to-pyroxene ratio between the Solomons arc and the New Hebrides arc, which includes both Vanuatu and the eastern outliers of the Solomon Islands as a political entity. Local basaltic tempers of the Santa Cruz Group at the northern end of the New Hebrides island arc and tempers derived from the post-orogenic basaltic cover rocks of Fiji plot in a position intermediate between the oceanic basalt and andesitic arc fields.

Pottery transfer

Although limited pottery transfer over comparatively short distances was probably common within complex island groups such as Fiji (Dickinson, 1971b), the transport of pottery over long distances was apparently not common within Oceania during prehistory (Dickinson *et al.*, 1996). Nevertheless, sherds with tempers exotic to the locales where they were collected provide welcome concrete evidence for pottery transfer in selected instances (Fig. 1). The places of origin of the exotic sherds can be identified with varying degrees of confidence in different cases. The most clearcut evidence for pottery transfer is provided by sherds containing volcanic sand temper that have been found at a number of atolls and raised-coral islands where only calcareous sands are present locally. Distinctive New Caledonian tempers (Galipaud, 1990) have been identified in ancient sherds from both the Loyalty Islands (Huntley *et al.*, 1983) and Vanuatu (Dickinson, 1971a), and sherds of wares apparently

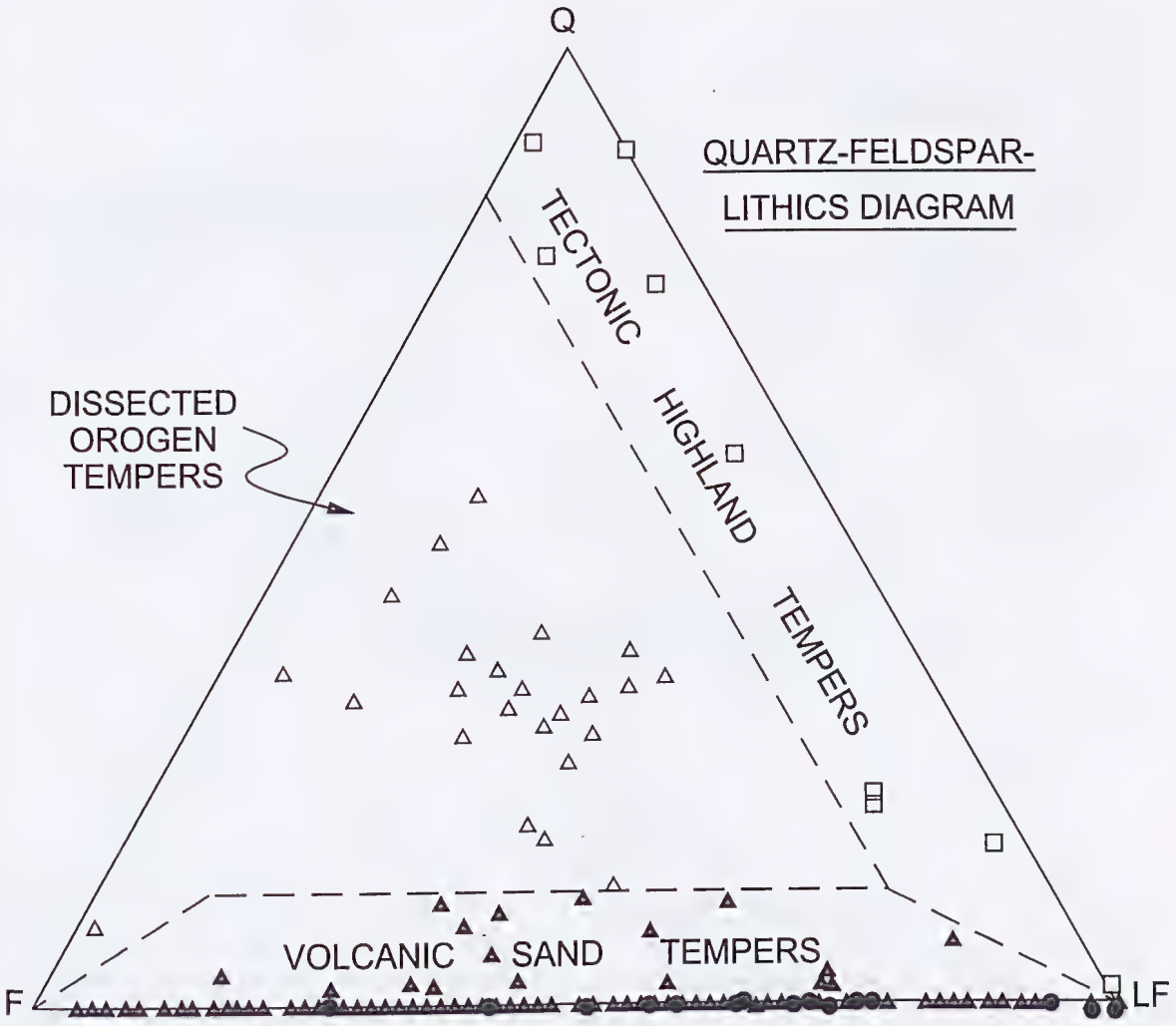

Figure 5. Triangular Q-F-LF plot of partial temper grain populations (all FM constituents of Figs. 2–4 excluded by recalculation), where Q = quartz grains, F = feldspar grains, and LF = polycrystalline-polyminerallic lithic fragments. Plotted points are average compositions of individual temper types, and empirical generic divisions are delineated between fields for dissected orogen, tectonic highland, and volcanic (oceanic basalt and andesitic arc suites undivided) temper classes.

manufactured on the Rewa Delta (Viti Levu, Fiji) have been recovered from protohistoric or uncertain contexts in Lau, Tonga, and the Marquesas (Dickinson & Shutler, 1974; Dye & Dickinson, 1996; Dickinson *et al.*, 1996). Wholly intrusive wares from outside the region are represented by colonial Spanish and Japanese Jomon sherds discovered in the Solomon Islands and Vanuatu, respectively, and contain entirely unfamiliar temper sands (Dickinson & Green, 1974; Sinoto *et al.*, 1996).

General conclusions

Oceanian tempers can be divided into broad classes correlated with geotectonic setting, and empirical differences between tempers from different locales within major temper provinces allow still further subdivision. Recognition of contrasting temper types and suites is not dependent on quantitative mineralogical differences alone, but rests primarily upon qualitative petrological differences that are evident without statistical manipulation of compositional data. Enough geologic information is now available about most island groups to allow evaluation of temper sources without ancillary collections of modern sands. Although comparative empirical data from modern sands is helpful for the interpretation of ancient tempers, truly exotic tempers can be detected petrographically without specific comparative materials.

Indigenous temper suites from many locales include multiple temper types forming a spectrum of beach and stream, placer and non-placer, or calcareous and non-calcareous sands. The megascopic appearance of closely related tempers may be highly variable as proportions of associated grains of different colouration vary. Only petrographic study can establish unequivocal generic similarities or differences among various indigenous and exotic Oceanian tempers.

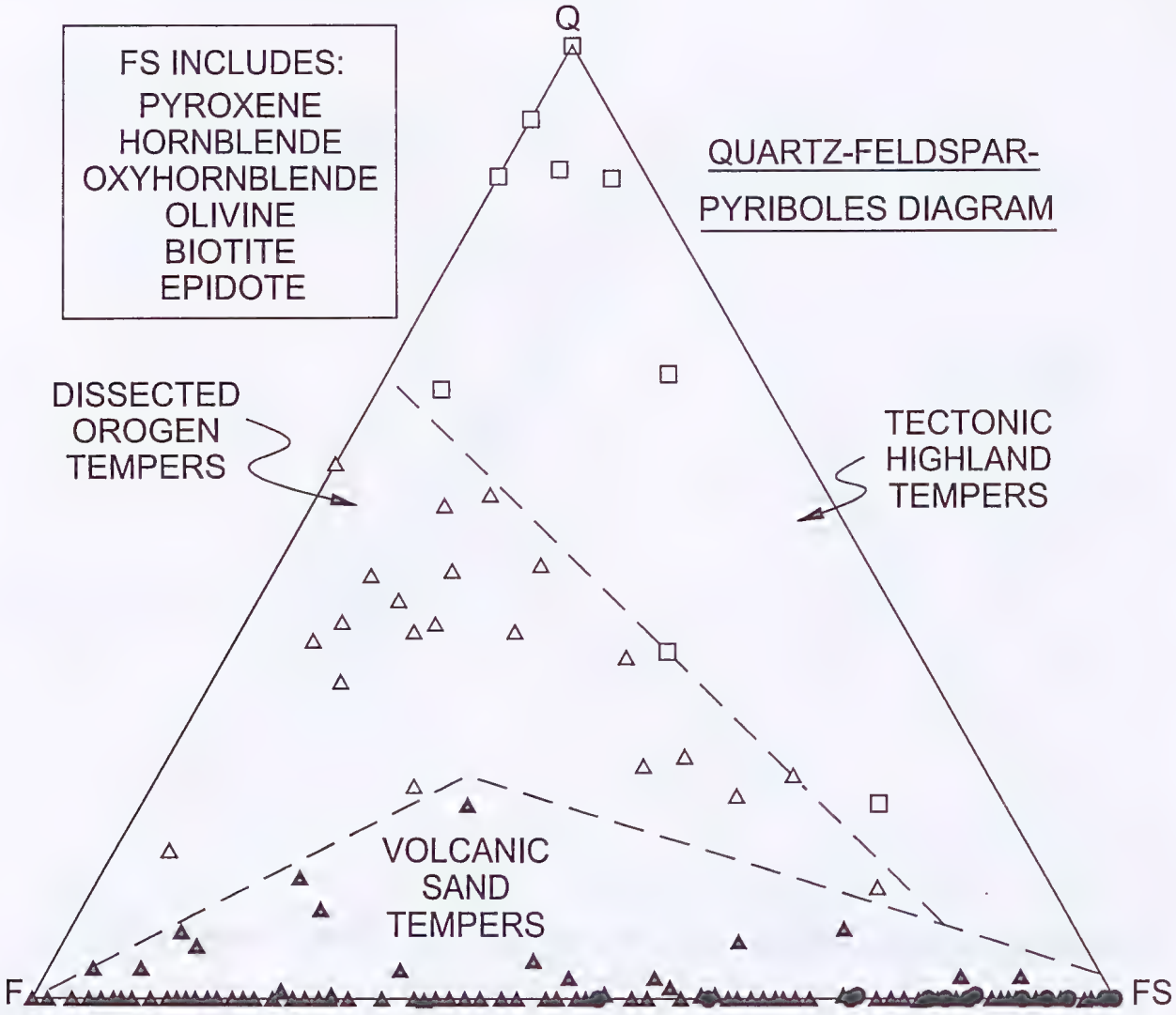

Figure 6. Triangular Q-F-FS plot of partial temper grain populations (recalculated for non- opaque mineral grains only), where Q = quartz grains, F = feldspar grains, and FS = ferromagnesian silicate grains (see Fig. 4 for identity). Plotted points are average compositions of individual temper types, with the compositional space divided into the same generic fields as for Figure 5.

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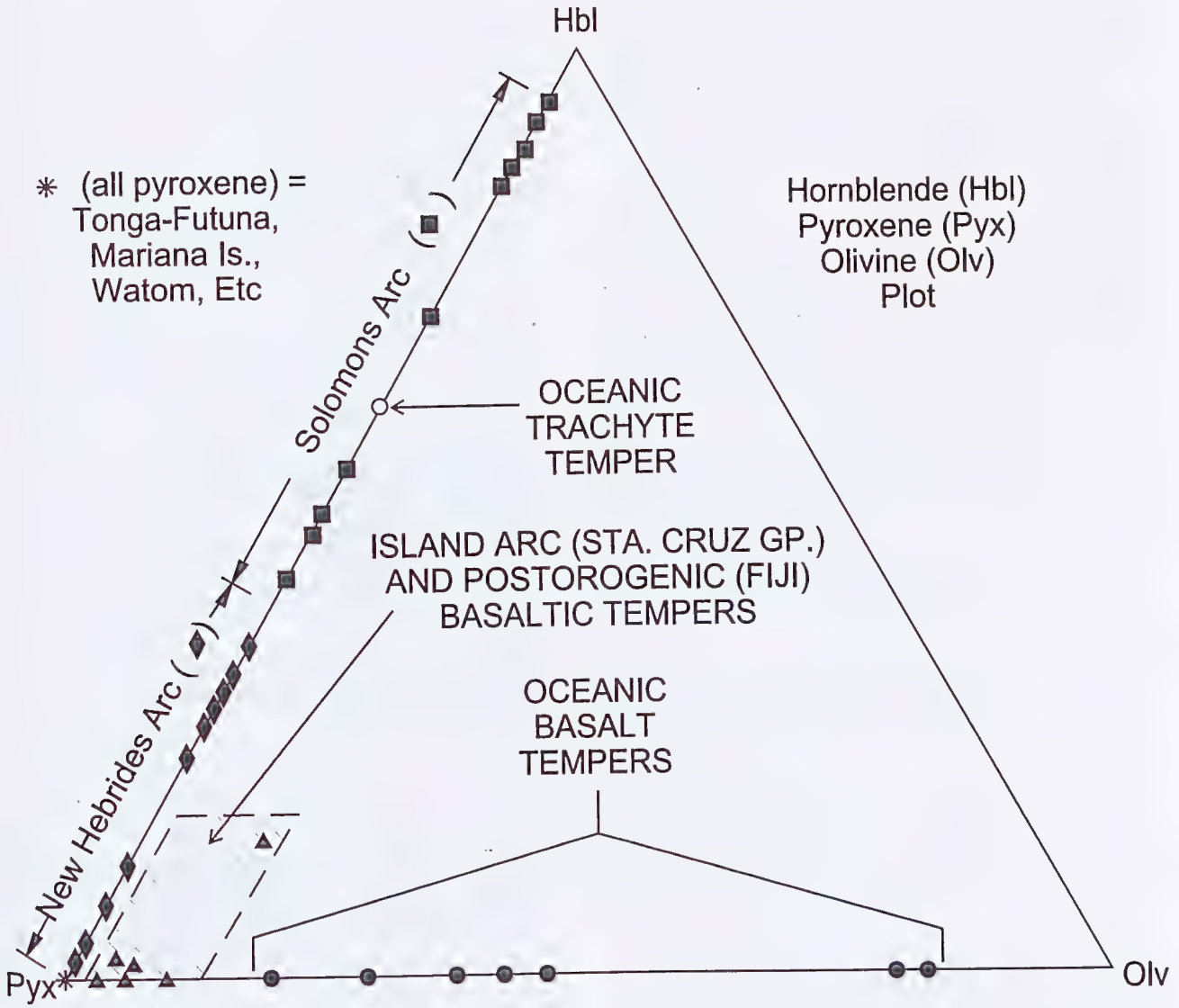

Figure 7. Average proportions of hornblende (hbl), pyroxene (pyx), and olivine (olv) mineral grains in selected oceanic basalt and andesitic arc tempers plotted on a triangular diagram to illustrate generic distinctions in hbl-pyx-olv space.

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Fission Track Dating of Obsidian Source Samples from the Willaumez Peninsula, Papua New Guinea and Eastern Australia

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Abstract. Obsidian samples from several outcrops in Papua New Guinea and eastern Australia have been dated by the fission track method for the first time. The Papua New Guinea samples yielded young ages (≈25 Ka), whereas dates of 85.5 Ma to 92.3 Ma were obtained for the Australian samples after using the plateau age and track size methods to correct for track fading. The archaeological implications of the fission track dates are discussed.

Bonetti, R., P. Di Cesare, A. Guglielmetti, F. Malerba, E. Migliorini, M. Oddone, J.R. Bird, R. Torrence & R.J. Bultitude, 1998. Fission track dating of obsidian source samples from the Willaumez Peninsula, Papua New Guinea and eastern Australia. *Records of the Australian Museum* 50(3): 277–284.

During the last two decades Fission track dating of obsidian has assisted provenance studies of prehistoric artifacts and the chronological study of related volcanic activity. For example, intense investigations have been carried out in the Mediterranean and nearby regions (Bigazzi *et al.*, 1982, 1990, 1993). This approach is applied here to Papua New Guinean and Australian obsidians to supplement archaeological studies of raw material sources and prehistoric trading patterns using trace element analysis (Bird *et al.*, 1987; David *et al.*, 1992; Torrence *et al.*, 1992, 1996; Summerhayes *et al.*, 1993, 1998). This paper aims to contribute to a more complete characterisation of sources and an improved understanding of their geological history by providing the first age determinations for some Papua New Guinean and Australian obsidians.

Background

Papua New Guinea Sources. The widespread distribution of obsidian artifacts in archaeological sites in the Pacific region in places distant from known sources of the raw material has been interpreted as evidence for prehistoric trading systems (cf. review in White, 1996). As part of a wider investigation of prehistoric obsidian trade, the natural occurrence of obsidian has been studied for a number of areas, but the most detailed work has been carried out in the Willaumez Peninsula region of West New Britain province in Papua New Guinea where four source areas have been identified: Kutau/Bao, Gulu, Baki and Hamilton (Torrence *et al.*, 1992, 1996; Summerhayes *et al.*, 1998).

The known distribution of obsidian sources in the Willaumez Peninsula, including both rhyolitic flows and associated secondary contexts, is reported in Torrence *et al.*, 1992. In addition to mapping the sources, a chemical analysis of obsidians from the four distinct source areas using the PIXE-PIGME technique has shown that they are distinctive (Bird *et al.*, 1997; Torrence *et al.*, 1992; Summerhayes *et al.*, 1993, 1998).

Characterisation of artifacts from numerous archaeological contexts using PIXE-PIGME has shown that throughout prehistory the Kutau/Bao source was predominant both within the local area and in the wider Pacific region (Summerhayes *et al.*, 1993, 1998). The presence of Kutau/Bao obsidian within levels dating between 18,000 and 20,000 B.P. at Matenbek cave in New Ireland is the earliest evidence for long-distance marine transport of material in prehistory (Summerhayes & Allen, 1993). Furthermore, the enormous spread of Kutau/Bao obsidian-extending from Sabah on the east to Samoa on the west-in the period between c. 3,500–2,000 B.P. is possibly the largest prehistoric distribution network known (Bellwood & Koon, 1989; Summerhayes *et al.*, 1993, 1998).

In direct contrast to the Kutau/Bao obsidian, almost no material from the other three obsidian sources was exported out of the region; however, material derived from them was used at archaeological sites situated quite close to the outcrops (Summerhayes *et al.*, 1993, 1998; Torrence & Summerhayes, 1997). Fission track analyses were carried out on one sample from the Kutau/Bao source (T6) and one from the Baki source (G002) (see map and descriptions in Torrence *et al.*, 1992). These samples were chosen because, like the histories of their use as shown by archaeological research, it was suspected that their geological histories differed.

The aim of the analyses, therefore, was to broaden our knowledge of the volcanic history of the region as well as to resolve several archaeological questions. Firstly, because the Kutau/Bao obsidian occurs within a rhyolite dome showing relatively little erosion, a young age was suspected. It was important to determine the chronological relationship between the age of obsidian formation and its first occurrence in archaeological sites in New Ireland. Secondly, the Baki obsidian was suspected to be older than the Kutau/Bao obsidian because it was derived from a poorly preserved caldera (Bird *et al.*, 1997). Dating the volcanic event which produced the Baki obsidian would help to determine the history of human settlement in the region in relation to volcanism.

The earliest date for human presence in West New Britain (c. 35,600 B.P.) is from the site of Yombon in the interior of the island. It is significant that obsidian does not occur in Pleistocene levels at this site (Pavlides & Gosden, 1994). If the Willaumez Peninsula was undergoing major volcanic activity during the period of initial settlement, it might explain why obsidian was not distributed from the region until much later.

Australian Sources. Although rare, outcrops of silicic volcanic glass are scattered through eastern Australia. They are variously referred to as obsidian, pitchstone, perlite, or vitrophyre depending on individual characteristics such as extent of devitrification and hydration, abundance of crystals, and presence or absence of conchoidal fracture or perlitic cracks. The glassy rocks are generally of limited extent and are collectively referred to as "obsidian" here for the sake of simplicity. The rapidly chilled margins of some high-level silicic intrusives and dykes also consist of obsidian in places, for example, west of Eidsvold (Burnett region of central Queensland, in a tributary of Morrow Creek, at GR 930 876, Rawbelle 1:100 000 Sheet area), in the Peak Range area (Emerald region of central Queensland, e.g., Knutson, 1989: 101), and in the Mitchell River area of far north Queensland (Bultitude *et al.*, 1996: 43).

Obsidian is most common in relatively young (Cainozoic) deposits. However, extensive outcrops of glassy dacitic ignimbrite of early Carboniferous age (332±4 Ma) from the Port Stephens area (near Newcastle) on the central coast of New South Wales have been described by Hamilton (1992) as the oldest abundant glass on Earth. He also listed other occurrences of relatively old (pre-Tertiary) volcanic glass (both silicic and basic varieties) in Australia and overseas. Subsequently, small outcrops of older obsidian were located west of Emerald in central Queensland in the Silver Hills Volcanics (Withnall *et al.*, 1995: 85) which is Late Devonian/early Carboniferous in age (≈370 to ≈340 Ma; Henderson *et al.*, in press).

Obsidian is relatively common in some late Palaeozoic (mainly Permian) volcanic sequences of north Queensland (e.g., see Hamilton, 1992; Mackenzie, 1993; Bultitude *et al.*, 1995, 1996). The samples of obsidian from far north Queensland (FNQ) dated here are from two rhyolite lava flows in the Early Permian Nychum Volcanics (Nolan Creek sample locality at GR 101397, Elizabeth Creek sample locality at GR 184423, Bellevue 1:100 000 Sheet area; cf. David *et al.*, 1992; Fig. 1). This geological formation contains extensive zones of obsidian in places. Samples AU602, AU603, and AU662 from outcrops in the headwaters of Nolan Creek and sample AU612 from Elizabeth Creek were analysed by the fission track method.

Obsidian artefacts have been found more than 30 km south of the Nolan Creek and Elizabeth Creek localities at an archaeological site called Echidna's Rest. PIXE/PIGME analyses performed at the Australian Nuclear Science and Technology Organization (David *et al.*, 1992) have shown the artefacts to be very different in composition to the widely studied Melanesian sources but chemically similar

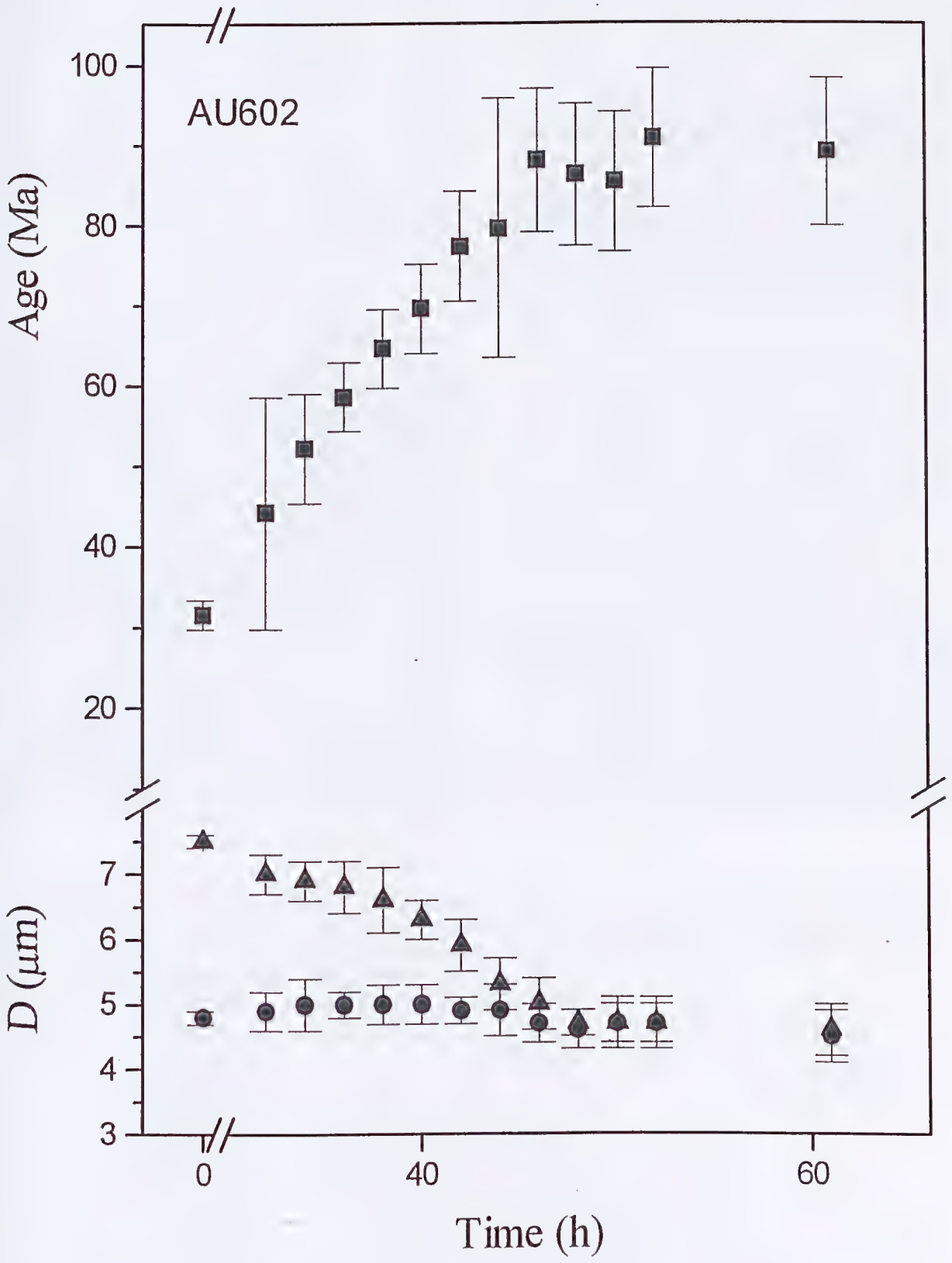

Figure 1. Plateau age for Australian obsidian AU602 obtained by using isothermal treatment (upper represented by squares). Induced (pyramids) and spontaneous (circles) fission-track diameters at each step of thermal treatment (lower).

to the Nolan Creek obsidian. Since the Nolan Creek source area extends over several square kilometres, whereas the Elizabeth Creek obsidian is very restricted because it is the chilled margin of a large rhyolite lava flow, it seems likely that the the former is the main source for the glassy artifacts.

Obsidian samples AU101 and AU102 were collected as isolated cobbles in streams in the Mount Warning area, in northern New South Wales (NSW). The late Oligocene/ early Miocene (≈24 to ≈21 Ma) Mount Warning volcanic sequence is much younger than the Nychum Volcanics. It also contains rhyolite lava flows, some with glassy bases and tops up to ≈10 m thick (Ewart *et al.*, 1987; Stevens *et al.*, 1989). PIXE-PIGME analyses have shown that this obsidian forms a well-defined compositional group, distinct from the other analysed sources in the southern Pacific (Bird *et al.*, 1987). No confirmed artefacts have been identified, probably because of the badly weathered nature of most of this obsidian, which is also commonly extensively devitrified.

Several obsidian artifacts have also been found in south-eastern Australian, but PIXE-PIGME analyses have been unsuccessful in linking them to known outcrops (Duerden *et al.*, 1987).

Fission track methods

The obsidian samples were divided in two fractions, one of which was irradiated at the Lazy Susan facility (Cd ratios 6.5 for gold and 48 for cobalt) of the Triga Mark II Reactor of the LENA Laboratory of the University of Pavia, Italy. Metallic monitors and CN1 and CN2 standard glasses, together with calibrated mica and Makrofol foils acting as external detectors were also irradiated for thermal neutron fluence determination; results are shown in Table 1.

After irradiation, the irradiated and non-irradiated fractions were prepared for etching and microscope observation. The standard technique consisting of mounting samples in epoxy resin, followed by grinding and polishing did not work for the NSW samples due to their almost completely crystallised condition. In this case, an appropriate technique had to be developed. Thin slices were cut with a diamond wheel, glued onto microscope slides and finally the cut surface was carefully polished Subsequently, etching was performed with 20% HF at T = 40°C for 70–120 seconds, and then spontaneous and induced fission tracks were observed and counted at 500× magnification.

Results

The Papua New Guinea results are shown in Table 2. Their young age caused no appreciable fading effect but, as a kind of perverse compensation for the experimentalist, fossil tracks were extremely scarce due to the very small (≈1 ppm) uranium content of the obsidians. The quoted uncertainty (≈30%) therefore reflects the relatively small number (11–15) of fossil tracks measured.

The Australian results are presented in Table 3. It is important to point out that the spontaneous to induced track size ratio, Ds/Di, is generally smaller than unity. This indicates considerable fading, producing lowered fission track ages. Standard thermal based correction techniques have therefore been applied. However, the conditions of the samples (crystallisation and devitrification for NSW samples and evidence for hydration for FNQ ones) imposed restrictions and concern. Subsequent experimentation at different temperatures and times has shown that only a low-temperature isothermal treatment was tolerable for the FNQ samples, while the NSW samples could not allow any temperature increase.

Table 1. Measurement of thermal neutron fluence.[1]

monitor	external detector	B (10^9 n t^{-1})	track density on ext. detector (10^5 t cm^{-2})	thermal neutron fluence (10^{15} n cm^{-2})
Au wire	–	–	–	2.399 ± 0.034
Co wire	–	–	–	2.392 ± 0.025
CN1 glass	mica	1.873 ± 0.025	13.43 ± 0.26	2.515 ± 0.036
	makrofol	1.863 ± 0.023	13.24 ± 0.26	2.468 ± 0.058
CN2 glass	mica	1.985 ± 0.007	12.34 ± 0.25	2.449 ± 0.051
	makrofol	2.016 ± 0.041	12.31 ± 0.25	2.482 ± 0.072

1 Calibration of glass dosimeters (B value measurement) was performed by using cobalt and gold monitors (Bonetti *et al.*, 1994). The thermal neutron fluence value used in the age measurements has been obtained as a weighted mean of the values listed in the last column.

Table 2. Results for fission track dating of Papua New Guinean obsidians.[1]

sample	n_s (t)	spontaneous track density (t cm^{-2})	n_i (t)	induced track density ($\times 10^4$ t cm^{-2})	neutron fluence ($\times 10^{15}$ n cm^{-2})	age ± (a)
Baki	11	17	2933	5.54	1.644 ± 0.014	30198 ± 8906
Kutau	15	14	7094	5.16	1.644 ± 0.014	26707 ± 7688

1 n_s and n_i represent the number of spontaneous and induced tracks counted, respectively. The induced track density has been evaluated by means of the population subtraction method. Ages are calculated by using the following constants ($\lambda_\alpha = 1.551 \times 10^{-10} a^{-1}$, $^{238}U/^{235}U = 137.88$, $\sigma_f = 580.2$ b, $\lambda_f = 7.03 \times 10^{-17} a^{-1}$). The thermal neutron fluence is determined from both two calibrated mica and Makrofol detectors in contact with glass dosimeters (Corning CN1, CN2) and two metallic monitors (Co, Au). All corrected ages are weighted means of values in the plateau region.

Both the "plateau" technique and the "correction curve" technique (Storzer & Wagner, 1969; Storzer & Poupeau, 1973; Arias *et al.*, 1981) have been applied to the FNQ samples. The results of the isothermal treatment at from 10–60 h is shown in Fig. 1. As can be clearly seen, the plateau age of 85 Ma is reached at 50 h, this time consistently corresponding to the attainment of the condition Ds/Di = 1 (lower part of Fig. 1), which indicates that thermal history of the fossil tracks has been reproduced for those induced in the laboratory. Corrected ages are shown in the last column of Table 3.

Discussion

Papua New Guinea Sources. The fission track dates presented in Table 1 not only provide new information about the volcanic history of the region, but also shed light on the nature of prehistoric human settlement in West New Britain and obsidian trade in the wider region. Although the Baki source is relatively old as suspected, at one standard deviation the dates for both obsidians significantly overlap with the earliest date for settlement in the region and with the earliest known use of obsidian in New Ireland. It seems likely that the absence of obsidian at Yombon during the Pleistocene may be explained by the absence of obsidian in the Willaumez Peninsula region until a later date and/or the difficulty of obtaining access to a highly active volcanic region. If the Willaumez Peninsula was undergoing major volcanic activity, as is evidenced by the caldera forming event which introduced Baki obsidian, then humans may have avoided the area until it was safe to explore. The initiation of obsidian movement at c. 20,000 B.P. may simply reflect the period when access to the sources became feasible. The beginning of marine transport of obsidian may therefore merely indicate when obsidian was first available to be exploited, and not a major change in social organisation/trading patterns or in boat technology

Table 3. Results of fission track dating of Australian obsidian samples; n_s, n_{i+s} represent the number of spontaneous and induced+spontaneous tracks being counted, respectively. See Table 2 for constants. (*) In this case the corrected age is determined by using the correction curve of sample AU602.

sample	n_s (t)	spontaneous track density ($\times 10^4$ t cm^{-2})	n_{i+s} (t)	induced track density ($\times 10^5$ t cm^{-2})	neutron fluence ($\times 10^{15}$ n cm^{-2})	Ds/Di	apparent age ± σ (Ma)	heating hours at 140°C	corrected age ± σ (Ma)
Far North Queensland (FNQ)									
AU602	2533	8.17 ± 0.16	3736	3.51 ± 0.07	2.431 ± 0.016	0.63 ± 0.06	33.9 ± 1.1	60	86.9 ± 3.8
AU603	1390	7.25 ± 0.19	3666	3.23 ± 0.07	2.431 ± 0.016	0.54 ± 0.05	32.7 ± 1.3	(*)	88.5 ± 9.0
AU612	278	10.86 ± 0.65	1002	4.13 ± 0.15	2.431 ± 0.016	0.68 ± 0.07	38.2 ± 3.2	(*)	92.3 ± 10.6
AU662	122	4.24 ± 0.38	608	1.69 ± 0.09	1.644 ± 0.014	0.53 ± 0.10	24.7 ± 3.1	70	85.5 ± 5.9
New South Wales (NSW)									
AU101	273	2.32 ± 0.14	898	2.57 ± 0.09	2.431 ± 0.016	0.79 ± 0.06	13.1 ± 1.0	–	–
AU102	95	1.48 ± 0.15	760	2.23 ± 0.09	2.431 ± 0.016	–	9.7 ± 1.1	–	–

as previously postulated (Summerhayes & Allen, 1993).

Fission track dating of two obsidian sources in the Willaumez Peninsula, Papua New Guinea therefore raises very important questions concerning the cause for the earliest long distance transport of raw material in world prehistory. Before the reasons for the inception of this transport can be fully understood, the distribution and nature of the obsidian sources themselves must be known. As several Pacific archaeologists have noted (Ambrose *et al.*, 1981; Torrence *et al.*, 1996), obsidian sources are impermanent; they are created at different times and are not always accessible due to sea level changes and volcanic activity. If the Willaumez Peninsula sources were unavailable for human exploitation until c. 20,000 B.P., then obsidian movement may not be the earliest evidence for human transport of raw materials over long distances. It may only represent the first archaeological signature of what was a much older phenomenon.

Additional dates on the two remaining Willaumez Peninsula sources, Gulu and Hamilton, as well as the very important source at Mopir (artifacts from there also occur in the early New Ireland sites), will provide very useful additional information about the nature of raw material availability during prehistory. It is against this background that archaeology can better understand the cultural history of obsidian trade (Torrence *et al.*, 1996).

Australian Sources. As Table 3 shows, the fading correction considerably increases the apparent fission track ages and also decreases their apparent spread. As a result, the three age-corrected FNQ samples exhibit a common value in the order of 85–90 Ma years, although derived from two physically different sources (AU612 from Elizabeth Creek, and AU602 and AU662 from Nolan Creek) that have different uranium contents (see Table 3).

The apparent fission track (AFT) ages of the obsidian samples from north Queensland are significantly younger than their stratigraphic age. The rhyolite lava flows from which the samples were obtained form part of the Nychum Volcanics of Early Permian age (Bultitude *et al.*, 1995). Another sample from the lava flow from which sample AU612 was collected recently yielded a U-Pb zircon ion probe (SHRIMP) age of 277±4 Ma (Bultitude *et al.*, 1996). This date represents the time of lava eruption and is consistent with the local stratigraphy. The Nychum Volcanics are unconformably overlain in places by latest Jurassic?/Early Cretaceous (Neocomian—late Albian; Smart *et al.*, 1980) sedimentary rocks of the Carpentaria Basin succession.

The AFT ages therefore reflect post-depositional heating and subsequent cooling in the Late Cretaceous. Significantly, several AFT ages in the range from ≈80 to ≈95 Ma have also been obtained from other pre-Late Cretaceous rock units in the Cairns hinterland (unpublished data of RJB). The elevated palaeotemperatures may have resulted from heating due to burial beneath the sediments of the Carpentaria Basin.

The cooling episode in the Late Cretaceous probably followed significant uplift, heating, and subsequent erosion of the region. Major changes in base levels and associated large-scale denudation between ≈110 Ma and ≈80 Ma have been recorded over much of southern, eastern and northeastern Australia, as well as in Papua New Guinea (e.g., Veevers *et al.*, 1991; O'Sullivan *et al.*, 1996; Raza *et al.*, 1996; Symonds *et al.*, 1996). These changes resulted from the onset of extensional thermal rifting on the eastern and southern margins of the Australian continent (Veevers *et al.*, 1991) related to the breakup of eastern Gondwanaland.

Conclusions

The fission track dating of Papua New Guinean and Australian obsidian sources has yielded valuable insights into the geological histories of these two regions. The New South Wales results demonstrate the importance of using suitable obsidian for studying older materials and the necessity of applying corrections for fission track fading in older obsidians.

In terms of archaeological implications, it is important to note that extremely old sources of obsidian, such as those in Australia, may still produce some workable material which may have been used in the past. Most Australian obsidians are not suitable for manufacturing tools, but some were exploited on a limited basis (David *et al.*, 1992). The fission track dating method did not yield the age the obsidians were formed, but the younger dates may indicate periods of reheating due to burial, magmatic activity, tectonism or a combination of these processes. As such, fission track dating may assist in unravelling the geological history of the region.

In contrast, the fission track dates of Papua New Guinean obsidians raise important implications about the history of trading systems and sea travel in this region. If obsidians from the Willaumez Peninsula were not formed until after the region was first settled, then their absence in the oldest archaeological levels is not indicative of the movements of people and raw materials at that time. In other words, the subsequent introduction of obsidian into archaeological sites could simply be a product of its availability rather than a change in human technology and/or social systems. Fission track dating of other Pacific obsidian sources could also help clarify the relationship between supply and demand within prehistoric economic systems.

Fission track dating also has potential as another technique for characterising obsidian outcrops and matching artefacts with their sources, as has been done successfully in the Mediterranean (e.g., Bigazzi *et al.*, 1990). With more work to apply an age correction to the NSW samples, it may be possible to use fission track dating to characterise Australian obsidian sources since the Ds/Di ratios in Table 3 indicate that the dates for the two areas would be distinctive. This would not be the case, however, for the two Papua New Guinean obsidians since the dates overlap at one standard deviation. These results provide further evidence that fission track dating has a potentially important role to play in geological and archaeological research.

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Radiocarbon Determinations on Chillagoe Rock Paintings: Small Sample Accelerator Mass Spectrometry

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ABSTRACT. Indirect dating methods have previously been applied to the rock paintings of north Queensland, utilising patterns of superimposition, depictions of material items and animals of known antiquity, the use of fragile paints such as mud and white kaolinite, and *in-situ* pigment stratigraphies. These patterns suggest that the vast majority of Chillagoe rock paintings are relatively young, likely less than 3500 years old. We directly analysed radiocarbon in the charcoal pigments in several of the Chillagoe rock paintings. Preliminary radiocarbon results at three sites confirm that these charcoal paintings are less than 3500 years old, as predicted. A change in the geographical distribution of rock art styles across north Queensland—from widespread non-figurative forms (as evident in surviving petroglyphs) to regionally distinctive motifs—suggests a regionalisation of artistic conventions starting around 3500 years B.P. Such a regionalisation implies that major cultural changes accompanied the changes in rock painting styles.

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Behavioural diversity is one aspect of the human condition that makes archaeology possible; it is the desire to characterise, model and understand both spatial variation in human behaviour, and its short- and long-term dynamics through space and time, that underlies this project. This is also the source of our methodological anguishes: how can we measure or otherwise describe past human activities, their spatial variability, and their trends at various temporal scales?

This paper is an exploration of method firmly rooted in this broader problem. Specifically, rock art is a manifestation of cultural activity. It is a cultural expression embedded in

the social, political, economic and psychological circumstances of its creator(s). Each picture, or part thereof, was created some time in the past, and through time certain artistic conventions changed while others remained the same. While representing the actions of particular individuals at specific places and times, individual items of rock art thus also articulate cultural conventions of those times. Rock art is, therefore, not only amenable to spatial and temporal analyses, but through space and time it is also suitable for the investigation of cultural patterning and dynamics.

However, rock art is also notoriously difficult to date; thus it is not easily situated archaeologically. Individual items of rock art were usually created either by adding specific substances to rock surfaces (pictographs, such as paintings), or by taking away parts of the rock (petroglyphs, such as abrasions or peckings). It should be possible, therefore, to date the age of a particular artistic creation by either dating the addition of materials to a surface, or its subtraction; in both cases it is the *event* which we would like to date. In the case of the former, pigments can themselves consist of organic compounds, such as charcoal or other plant colours, which are amenable to radiocarbon dating. In other cases, the presence of organic binders or other intrusions (e.g., filaments from paint brushes) may offer the opportunity to date the pigments directly. In the case of petroglyphs, organic materials caught both beneath and above the modified surface may give maximum and minimum ages to the artistic event.

Unfortunately, the dating of the artistic event is more complex than this, as there are various potential factors complicating the issues. Some of these concern the antiquity of the organic materials when they were put on the wall, for example, the "old wood problem" in the case of charcoal drawings. Others involve sources of contamination, both in the form of fungi, algae and other organic activity, and in the intrusion of modern or ancient carbon through the activity of water, wind and the like. There is also the problem of retouching in ancient times, potentially adding layers of pigment through time. And last but not least, there is the real problem of extracting minute amounts of datable materials from a given rock surface.

This paper is a methodological contribution to the dating of rock art. As such, it is a contribution aimed at further exploring the ability of accelerator mass spectrometry (AMS) radiocarbon dating method to date charcoal drawings. It also aims to help elucidate the types of problems (and solutions) one may be confronted with when "directly" dating rock art. Although the case study presented here also forms an early stage in an attempt to understand the antiquity of the rock art of the Chillagoe region of northern Australia, at this stage the promising results obtained should be interpreted as much in terms of a methodological investigation as of a regional study.

The Chillagoe case study: background

Rock art is commonly found in many parts of northern Australia. Chillagoe is one such region, located some 120 km west of Cairns in north Queensland (Fig. 1). Archaeologically, Chillagoe can be divided into two temporal units (at a broad temporal scale): the period before ≈3500 years B.P., and that since (David & Chant, 1995).

Little is known of the earlier period. Of relevance here, however, is what appears to be a relatively homogeneous artistic tradition consisting of abstract motifs, including "star bursts", circles, pits, single lines as well as sets of lines. Non-figurative motifs such as these were clearly *engraved* on rock surfaces during this early period. Campbell & Mardaga-Campbell (1993: 59) have reported a single AMS radiocarbon age > 7085 ± 135 years B.P. for one pecked "sunburst" from Walkunder Arch Cave in the Chillagoe region, indicating the presence of very old motif forms similar to late Holocene paintings for the region. The degree to which such motifs may also have been painted or drawn is not yet clear. Campbell & Mardaga-Campbell (1993) and Watchman & Hatte (1996) have reported evidence of earth pigments laminated between ancient rock crusts at various sites around Chillagoe dating back to 28,100 ± 400 years B.P. The nature of the pictographs is yet unknown as they were revealed in cross-sectional studies of encrusted rock surfaces—are they paintings, prints or stencils? In addition, uncertainties still exist concerning the anthropogenic nature of these pigments and the sources of the dated carbon (extracted by laser ablation). However, this evidence implies that pigment art has been created in the Chillagoe region ever since people first arrived in the region despite their more common occurrence after 3500 years B.P.

Certainly, ochre crayons and other small fragments of ochre are far more common within excavated, stratified deposits after ≈3500 years B.P. than they were from earlier deposits. All in all, it appears that before ≈3500 years B.P. rock art in Chillagoe and elsewhere in north Queensland consisted principally of engraved, non-figurative motifs, although pigment art was also practised. The early rock art of Chillagoe is believed to be very similar both formally and technically to that of other regions in north Queensland, including the Mitchell-Palmer limestone zone, Laura and the Koolburra Plateau > 100 km to the north (David & Chant, 1995; see also Rosenfeld *et al.*, 1981).

The period after ≈3500 years B.P. saw major changes in the archaeological record of all parts of north Queensland. This was the time when dingoes first arrived in Australia; it was also the time when new stone tool types and technologies first appeared (e.g., systematic seed grinding stones, burren adzes, blades) (David & Lourandos, two manuscripts in press: *a, b*). Deposition rates of cultural items increased many-fold within individual sites, and the number of occupied sites across the landscape also increased markedly. Along with these changes came a major increase in the amounts of ochre dropped on ancient

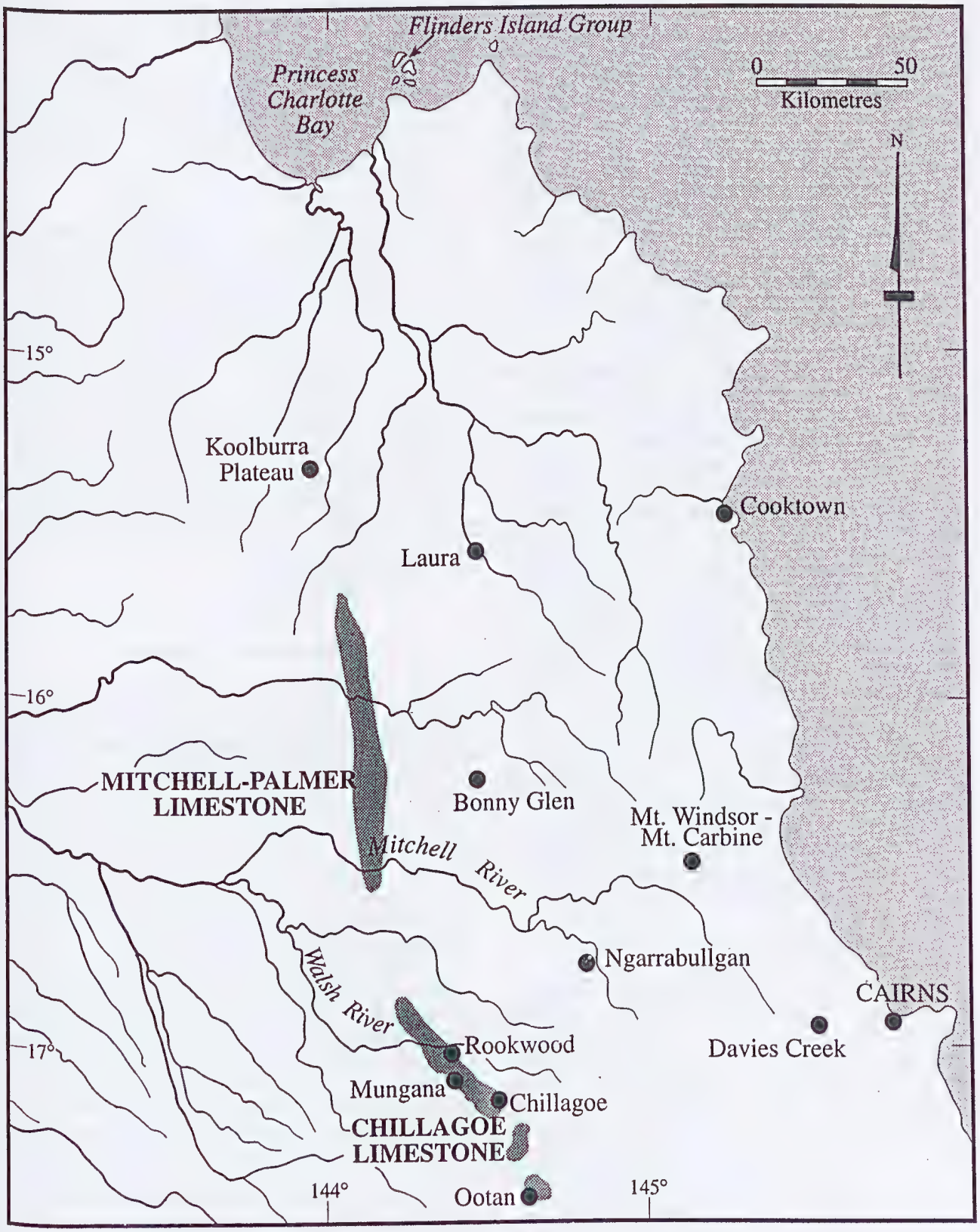

Figure 1. Map of northeastern Australia (Queensland) including the Chillagoe region.

floor levels within individual sites; the implication is that painting, drawing, stencilling and/or printing activity increased significantly. Together, these various lines of evidence, often indicating quantitative increases in the activities of people on the landscape, have been interpreted by archaeologists to indicate (among other things) probable and noticeable increases in intensities of land use during the mid to late Holocene. This was probably associated with population increases (e.g., David & Chant, 1995; Lourandos, 1997), although we are still uncertain about what caused these changes (but see David & Lourandos, in press, *b*).

But this quantitative evidence does not stand in isolation. While at Chillagoe motif forms do not appear to have changed noticeably after ≈3500 years B.P., in neighbouring regions to the north they did. At Laura, a unique set of conventions commonly referred to as "Quinkan" art probably dates to the last 3500 years (and especially to the last 2000 years) (Cole *et al.*, 1995; David & Lourandos, in press, *b*). In the Mitchell-Palmer limestone zone between Laura and Chillagoe, an extremely homogeneous body of paintings consisting almost entirely of monochrome or bichrome anthropomorphs emerged around this time (David & Chant, 1995; David *et al.*, 1997). In the Koolburra Plateau nearby, painting conventions were similar to those at Laura, but here endemic "human-echidna" pictures began to be painted (David & Chant, 1995; Flood, 1987). In each of these regions the archaeological evidence points to ages for the paintings during the mid to late Holocene. The indication here is that in addition to the quantitative changes noted above, the rock art attained a more regionalised configuration; the cultural landscape appears to have become divided in space in a way not previously evident. The implications for cultural (including social, political and economic) dynamics in north Queensland prehistory are major (David & Lourandos, in press, *a*).

Our understanding of the antiquity of the art is based, however, on rather poor, circumstantial evidence, although the various lines of evidence support rather than contradict each other (see David & Chant, 1995, for details). These include:

1. the occurrence of animals of known antiquity (e.g., dingoes, animals introduced by Europeans);
2. the presence of fragile pigments (e.g., white kaolinite, brown mud) in the art purported to be of late Holocene age;
3. peak deposition rates of ochre in the late Holocene layers of excavated sites with purported late Holocene rock art. The indications here are that most of Chillagoe's surviving paintings date to the last ≈3500 years B.P. It also implies that earlier times witnessed markedly lower levels of painting activity throughout north Queensland;
4. the few radiocarbon dates currently available for the art are in line with the above temporal model. All eleven radiocarbon dates for paintings and drawings obtained so far have revealed late Holocene ages. Late Holocene, as well as older dates, have been obtained for some engravings, indicating that engraving activity is both older than and contemporaneous with the period of painting/drawing activity (Campbell & Mardaga-Campbell, 1993; Morwood & Hobbs, 1995; Watchman & Cole, 1993) (see above);
5. patterns of superimposition are in agreement with the relative ages as outlined above (that is, paintings are always superimposed over *patinated* engravings; some unpatinated engravings, however, occur over paintings, indicating a continuity of engraving traditions until recent times). This is in line with 4, above.

To test the above temporal model, we initiated a systematic AMS radiocarbon dating programme on paintings and drawings of both Chillagoe and the Mitchell-Palmer regions. This testing is a high priority for a regional archaeology of north Queensland, given the major implications of the apparent changes in distribution of rock art forms across space in north Queensland (and indeed Australian) prehistory (see David & Chant, 1995, for an elaboration of these implications). If the model is sustained, a regionalisation of land use, territorial structures and inter-regional interaction may be implied. Qualitative changes in the organisation of Aboriginal people on the ground may be implicated for the mid to late Holocene; this restructuring of cultural landscapes may well be associated with population increases, given the quantitative changes outlined above.

We report below on our results from the Chillagoe study.

Experimental procedure

Samples were collected by BD and MWR from five separate charcoal rock paintings in five rock shelters in the Chillagoe region. All samples came from limestone outcrops, except for sample CM75-1, which came from a painting on a granite rock near Ootan towards the southern edge of the Chillagoe region. Sample CM2-1 is from a set of 14 radiating lines ("sunburst") (Fig. 2); CM55-1 is from a set of concentric arcs; CM56-1 is from a set of enclosed parallel lines; CM62-1 is from a set of sub-parallel lines immediately underlying an elongated red linear design (the latter hence post-dates the radiocarbon-dated design); and CM75-1 is from seven radiating lines ("sunburst"). Photographs were taken before and after sample removal. Particular care was taken to keep the visual effects of sampling to a minimum. A small area of each drawing was scraped onto a square of aluminium foil, each time using a sterile scalpel blade. The resulting powder was a mixture of limestone ($CaCO_3$) substrate, charcoal pigment and overlying accretion. New latex gloves were worn during collection of each sample and when handling the foil to prevent contamination. Enclosed in the foil, each sample was placed in a zipper-seal polyethylene bag, labelled and taken to the plasma-chemical laboratory at Texas A&M University. There they were photographed under magnification and weighed after foreign matter was removed: CM55-2, three short, white fibres; CM55-4, four white fibres; CM55-1, one black and one white fibre; and CM75-1, one fibre (no colour recorded).

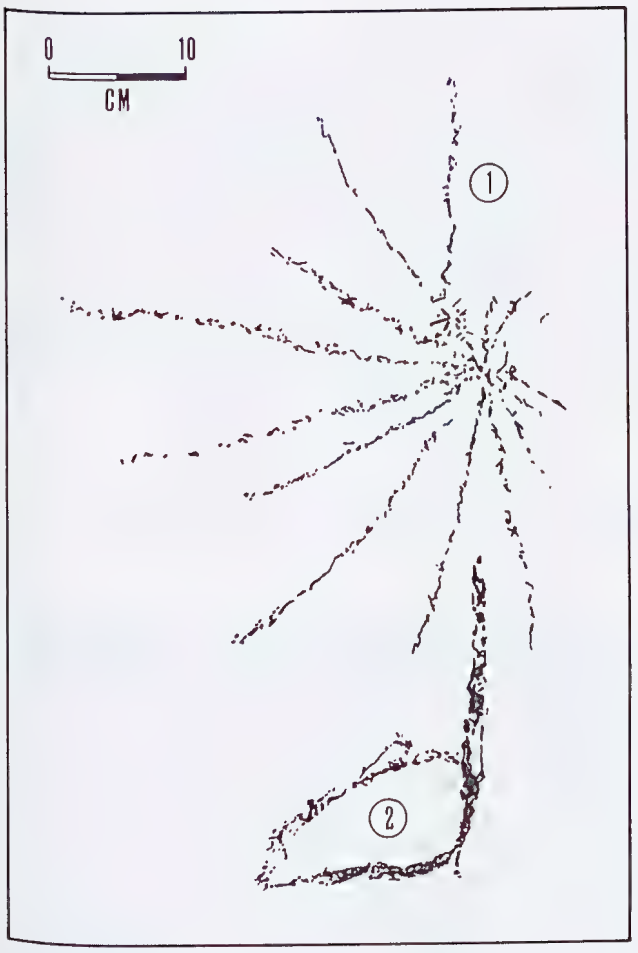

Figure 2. Tracing of the CM2-1 (top) and CM2-2 (bottom) rock drawings from Chillagoe. AMS radiocarbon results for CM2-1 are reported in Table 1.

Weights of total material ranged from 9 to 66 mg, with one exceptional sample that included large pieces of substrate limestone weighing 263 mg (CM62-1).

We use a radio frequency generated low-temperature (≈150°C), low-pressure (≈1 torr) oxygen plasma, coupled with high vacuum techniques, to remove organic matter in the rock painting sample; remaining carbonate or oxalate accretions do not decompose under these conditions (Ilger *et al.*, 1996 and references therein). Early studies in the Texas A&M University plasma-chemical laboratory established the efficacy for cleaning the plasma extraction system with oxygen plasmas before sample insertion to rid surfaces of organic contamination that may have been trapped in the chamber, as well as adsorbed CO_2 (Chaffee *et al.*, 1993).

A standard alkali (1 M NaOH) pretreatment was performed to remove possible contaminating humic acids from the charcoal pigments. Approximately 1 mL of 1 M NaOH was added to the sample in an ultracentrifuge tube and sonicated for 60 minutes at 50°C. After decanting off the alkaline solution, the remaining solid was sonicated at 50°C in dilute acid (0.1 M HCl) to reduce adsorption of atmospheric CO_2 and then rinsed in deionised distilled water. Solid remaining after this treatment was transferred to aluminium foil and dried overnight at 100°C. The treatment solutions from both steps were combined and saved; these solutions contained visible amounts of solid from the decanting step. After plasma treatment of the solids, the remaining solutions were vacuum filtered to recover as much charcoal as possible. Before use, the binder-free, glass-fibre filters were baked at 500°C overnight to remove organic contamination. The filtered material was then plasma-chemically treated separately to provide replicate analyses of the sampled material. The filters with the charcoal, background limestone and accretion were dried at 100°C prior to plasma chemical treatment; these vacuum-filtered samples are referred to as "filtrates". Samples CM55-1, CM55-1 filtrate and CM56-1 yielded less than 10 µg carbon and were not analysed for radiocarbon. Sample CM56-1 filtrate, yielded 70 µg carbon and was sent to Australian Nuclear Science and Technology Organisation (ANSTO), but gave no output (negligible ^{14}C counts and negligible ^{13}C current) on AMS analysis. This may have been a result of poor graphitisation.

The charcoal samples isolated from the Chillagoe rock paintings were removed from the filter and placed in the plasma reaction chamber under ultra-high purity (99.999%) argon maintained above ambient pressure. The system was sealed and the samples subjected to sequential low power radio-frequency argon plasmas. Though unreactive, the energetic argon atoms in the plasma remove surface-adsorbed CO_2 through inelastic collisions. When less than one µg carbon as CO_2 is desorbed via this process, the system is evacuated using oil-free sorption and ion pumps to $\approx 2 \times 10^{-7}$ torr. After this pressure has been maintained overnight, all pumping is stopped and any rise in the system pressure is recorded over time. If the pressure increase were all from CO_2, as we assume to provide a worst-case scenario, it can be converted using the ideal gas law to an equivalent weight of carbon. The maximum rise in pressure during a vacuum integrity check occurred with sample CM62-1; after 60 minutes, the system pressure rose to 1.0×10^{-4} torr. This corresponds to < 0.2 µg carbon even with the unrealistic assumption that all the pressure rise is due to CO_2. Because this corresponded to less than background levels of carbon from graphitisation (typically an upper limit of 1.1 µg carbon), they were always considered to be negligible. Plasma-chemical oxidation followed these vacuum integrity checks, using ultra-high purity (99.999%) oxygen passed through a liquid nitrogen-cooled finger to remove any contaminants from the gas fill line. The CO_2 and H_2O produced was collected in a 6 mm glass tube cooled to liquid nitrogen temperature (–194°C). Water was removed from the CO_2 using an ethanol-liquid nitrogen slush prior to refreezing the finger in liquid nitrogen; the tube was then removed by flame-sealing. The Chillagoe paint samples yielded from less than 10 up to 110 µg carbon as CO_2 (Table 1). Samples yielding less than 10 µg carbon were stored at Texas A&M University, as they are too close to the expected AMS background for reliability. Radiocarbon analysis was conducted on the other samples to investigate the reliability and accuracy of radiocarbon dates obtained on very small samples of carbon. The sizes

Table 1. Radiocarbon results for replicate analyses of five Chillagoe rock paintings.

sample	carbon (micrograms)	AMS ID	modern carbon %	^{14}C age (years B.P.)
CM2-1	45	OZB758	86.11 ± 4.69	1200 ± 440
CM2-1 filtrate	40	OZB783	65.93 ± 2.81	3350 ± 350
CM55-1	< 10	too small	not measured	–
CM55-1 filtrate	< 10	too small	not measured	–
CM56-1	< 10	too small	not measured	–
CM56-1 filtrate	70	OZB764	no output	–
CM62-1	15	OZB586	88.46 ± 5.33	990 ± 485
CM62-1 filtrate	95	OZB765	85.42 ± 2.59	1270 ± 250
CM75-1	75	OZB587	71.72 ± 2.6	2670 ± 290
CM75-1 filtrate	25	OZB782	77.96 ± 4.92	2000 ± 510

of our organic carbon samples analysed by the AMS (Table 1) were often less than the 100 µg typically needed for a reliable AMS analysis. The sealed glass tubes containing the CO_2 extracted from the paintings were shipped to the ANTARES AMS facility at ANSTO. The carbon dioxide was converted to graphite using a modification of the method of Jull *et al.* (1986). In a single tube, the carbon dioxide was reduced by iron catalyst (at 600°C) in the presence of zinc (400°C) and a small amount of hydrogen. The resulting graphite/iron mixture was loaded into aluminium holders for AMS measurement.

Results

Radiocarbon results are shown in Table 1. Filtrate samples provided additional results from each of the three samples analysed (CM2-1, CM62-1 and CM75-1). Large uncertainties reflect the poor statistical precision resulting from the low output (^{14}C counts and ^{13}C current) of small samples. We emphasise that the dates listed in Table 1 are dates for the charcoal; as always in archaeology, the charcoal age does not necessarily date the archaeological event desired, in this case the time of painting of the motif (the "old wood problem" [Schiffer, 1986]). However, in the Chillagoe region we argue that while it is possible that old charcoal was picked-up from ancient floor surfaces rather than created afresh for rock drawing, the "old wood problem" as conventionally defined—that is, that the wood itself was old before burning—is unlikely to be a major problem, given that in this part of north Queensland no species of tree lives more than a few hundred years. Once dead, plant material (including wood) does not last very long on the ground (again, a maximum of tens of years), given the tropical nature of the area and the activity of termites. Therefore, the difference between the age of the archaeological event and the time of burning of the wood may be of a few hundred years, but it is even more likely to be of the order of tens of years only.

More problematic in our case is the possibility that ancient charcoal was picked-up from old occupational surfaces, or even dug-up from below the ground within previously occupied rock shelters. This is a very difficult phenomenon to measure, although one noticeable characteristic of deposits prior to the late Holocene is a marked paucity of charcoal (along with lower amounts of all types of cultural materials). In many excavated sites in north Queensland (e.g., Fern Cave, Hearth Cave, Mitchell River Cave), charcoal is either extremely rare or totally absent from deposits dating to before ≈3500 years B.P. (David & Chant, 1995). Also, most archaeological rock shelters throughout north Queensland only have mid to late Holocene deposits; that is, there is no evidence for earlier occupation. Indeed, this is a common phenomenon across Australia (David & Chant, 1995). Furthermore, if pre-existing charcoal was picked-up from the old floor surface at the time of painting or drawing, it would date to the immediately previous time of occupation. Given the more or less continuous nature of sediment deposition on inhabited floor surfaces (albeit at varying rates), exposed floor surfaces are unlikely to be much older than the events that took place on them. Exceptions to this are generally relatively identifiable geomorphologically, such as in the southwest Tasmanian rainforests where ancient floor surfaces have remained exposed for many thousands of years (e.g., Porch & Allen, 1995). But even here lack of sediment deposition during "recent" times was due to an absence of human occupation during this time. There is no evidence of such sedimentation trends, cultural or geomorphological, in any of the sites investigated at Chillagoe, the Mitchell-Palmer, Laura or the Koolburra Plateau (David & Chant, 1995; Morwood & Hobbs, 1995). On the contrary, in each of the excavated sites the character of mid to late Holocene occupation appears to be more or less continuous, as measured at an archaeological time scale (i.e. one occupational event leads into another up the sequence; these are not easily differentiated in time via radiocarbon analyses). Given the above, we conclude that it is extremely unlikely that the charcoal examined from the rock drawings incorporate any significant degree (i.e. of more than ≈300 years at the most) of old wood problems, in any of the various senses described above.

Corrections were made to the radiocarbon ages for the background from graphitisation at ANSTO. We have conducted radiocarbon analyses of ^{14}C-free materials oxidised with the plasma-chemical technique, obtaining an average radiocarbon age of > 42,000 years B.P. The evidence suggests that negligible modern carbon is added by the plasma treatment (Ilger *et al.*, 1995).

To compare the two radiocarbon ages (the original solid left after decanting the NaOH solution and the solid filtered from the solution) for each of the three sets of samples, we used the statistical method described in Ward & Wilson (1978). In that method, the two ages are tested for difference using equation 1.

$$T = \sum (A_i - A_c)^2 / \sigma_i^2 \qquad (1)$$

(1) where T is the test statistic with χ^2 distribution for two dates, $\chi^2 = 3.841$. Thus if T is < 3.841, then the two dates are statistically indistinguishable and can be combined according to equation 2.

$$A_c = \sum (A_i / \sigma_i^2) / \sum (1 / \sigma_i^2) \qquad (2)$$

(2) where A_c is the combined (pooled) date, A_i are the individual radiocarbon ages and i values are 1 and 2, and σ_i are the uncertainties of the measurements. Thus the combined or pooled age is weighted as the inverse of the squares of the uncertainties of the measurements.

CM62-1 yielded an age of 990 ± 485 years B.P.; the solid remaining in the rinse solution (CM62-1 filtrate) yielded an age of 1270 ± 250 years B.P. Ward & Wilson analysis indicated that ages for these two replicates of CM62-1 were statistically indistinguishable. Agreement is striking in view of the fact that there was only 15 µg carbon in the smaller of the two. The combined age for CM62-1 calculated from equation 2 is 1210 ± 220 radiocarbon years B.P. CM75-1 was dated to 2670 ± 290 years B.P. as compared to 2000 ± 510 years B.P. for CM75-1 filtrate, again statistically indistinguishable. The combined age for CM75-1 is 2500 ± 250 radiocarbon years B.P. The ages for the two replicates of CM2-1 were different statistically (1200 ± 440 years B.P. for CM2-1 and 3350 ± 350 years B.P. for CM2-1 filtrate) and cannot be combined. We assume that the older of the two ages is more accurate based on the observation in the Texas A&M University laboratory that extremely small samples (such as our 15 µg samples from CM62-1) are more likely to be significantly affected than larger ones by minute amounts of modern contamination and yield younger results.

Conclusion

Although the number of dated samples is too small to carry statistical significance, these preliminary radiocarbon analyses confirm the expectation that the Chillagoe paintings studied here were painted within the past 3500 years (David & Chant, 1995). While we are encouraged that two of the three coupled samples reported here agree within statistical expectations with one another, we remain cautious and conclude that much more work remains before we can say that such small samples can be reliably analysed by AMS at ANSTO.

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Early Myriapodous Arthropods from Australia: *Maldybulakia* from the Devonian of New South Wales

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ABSTRACT. The myriapodous arthropod *Maldybulakia* Tesakov & Alekseev, 1998, was first described from the Lower Devonian (Pragian-Emsian) in central Kazakhstan. The geographic and stratigraphic distributions of *Maldybulakia* are broadened by the discovery of Devonian species in Australia. The Lochkovian or Pragian *Maldybulakia angusi* n.sp. occurs in abundance in the Sugarloaf Creek Formation near Taemas, NSW. *Maldybulakia malcolmi* n.sp. occurs in late Givetian or early Frasnian strata of the Boyd Volcanic Complex near Eden, south coastal NSW. Two trunk tagmata are present in *Maldybulakia*. The strong tergal exoskeleton of posteriorly overlapping diplopleurotergites suggests closest affinities with Dignatha and, particularly, Kampecarida. Along with arthropleurids and kampecarids, *Maldybulakia* represents another major myriapod bodyplan in the mid-Palaeozoic. Although occurring in lacustrine and fluvial sediments, the associated flora, likely myriapod affinities, and presence of spiracles in *Maldybulakia* suggest terrestrial habits.

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Myriapods have a sparse fossil record prior to the Carboniferous Period (see Almond [1985] and Shear [1990] for reviews of Silurian-Devonian body fossils). Among extant myriapod groups, millipedes and centipedes are known to have evolved by the Přídolí (Upper Silurian) (Almond, 1985; Shear *et al.*, 1998). Myriapodous fossils range back to the Lower Silurian (Mikulic *et al.*, 1985a,b), but the systematic position of these forms is uncertain. The extinct Class Arthropleuridea, best represented in the Upper Carboniferous (Briggs & Almond, 1994), extends back to the Přídolí, with new Devonian occurrences recently coming to light (Shear & Selden, 1995; Shear *et al.*, 1996). In spite of the patchy fossil record, several factors indicate that the major events in myriapod evolution had occurred by the Devonian. Among these is the cladistically derived position of Middle Devonian centipedes, which nest within some extant groups (Shear & Bonamo, 1988). Further, the Upper Silurian occurrence of Diplopoda predicts that the other extant lineages in the Progoneata and Dignatha, the Symphyla and Pauropoda, had diverged by that time (Kraus & Kraus, 1994).

Except for trace fossil indications (Trewin & McNamara, 1995), all that is known about Silurian-Devonian myriapods has come from the northern hemisphere, and in particular the Old Red Continent. The only citation of mid-Palaeozoic myriapods from Gondwana has been fraught with controversy. Bergström (1979: 9–10) mentioned "undescribed myriapod material from the

Silurian of Australia", but Almond (1985) cited the view of H.B. Whittington that this material was actually Devonian and its myriapod affinities were highly questionable. The present work documents this controversial material and provides a formal taxonomy based on extensive new collections.

H.B. Whittington (pers. comm., 1994, 1995) informed me that the enigmatic fossils in question were shown to him by K.S.W. Campbell. Campbell revealed that these arthropods were collected from an Early Devonian site in the Taemas-Wee Jasper district, New South Wales, and led a trip to the locality in 1995. Disarticulated sclerites of a large, apparently myriapodous, arthropod were found in the Sugarloaf Creek Formation in an abundance rivaled by few fossil myriapod sites. The species is described here as *Maldybulakia angusi* n.sp. Also in 1995, Alex Ritchie informed me of a Devonian site from which he had collected parts of a myriapodous arthropod near Eden on the south coast of New South Wales. Collecting at this locality revealed a second species of *Maldybulakia* Tesakov & Alekseev, 1998, and showed the genus to range into the Middle or Upper Devonian. This second species is named *Maldybulakia malcolmi* n.sp.

The Australian species are considered congeneric with the enigmatic myriapodous taxon *Maldybulakia mirabilis* (Tesakov & Alekseev, 1992), from the Lower Devonian of central Kazakhstan. The new material adds considerable clarity to the nature of tagmosis in this arthropod, and sheds more light on the affinities of *Maldybulakia*. While Tesakov & Alekseev (1992) employed descriptive terminology used for millipedes, they made no more precise systematic placement for the genus than to regard it as myriapod-like. Material at both Australian localities consists of trunk tergites and pleurotergites alone (the sternum and limbs were clearly less mineralised, and unpreserved). The heads of all three species are unknown. Tesakov & Alekseev (1992) interpreted the trunk tergites of *Maldybulakia* as diplosegments, divided into prozonites and metazonites. I have accepted this interpretation in describing the Australian species, for reasons elaborated below.

Specimens illustrated in this work are housed in the Palaeontology type collections of the Australian Museum (prefixed AM F.).

Occurrences

Localities, environments, and ages. *Maldybulakia* is at present known from two localities in the Devonian of New South Wales (Fig. 1).

Maldybulakia angusi occurs in the Sugarloaf Creek Formation, near the eastern outcrop limit of the formation. The site (35°04'S 148°51'E) is located about 400 m east of Mountain Creek Road, and is accessed 400 m south of Three Oaks homestead (Fig. 1C). The Sugarloaf Creek Formation consists of massive, lenticular arenites deposited in alluvial fans in the western part of the outcrop belt (towards Wee Jasper), but is composed of thinner, parallel-bedded arenites, siltstone and shale in the eastern extent where *Maldybulakia angusi* was collected (Owen & Wyborn, 1979). The fossils occur as totally disarticulated moulds in fine-grained sandstones rich in volcanic rock grains derived from the underlying Mountain Creek Volcanics. No other animal fossils have been found associated with *M. angusi* (only very rare plant fragments), yet this single species is sufficiently abundant as to locally litter bedding surfaces. The depositional environment of the arenites in the eastern extent of the Sugarloaf Creek Formation has been interpreted as fluvial (Owen & Wyborn, 1979). Although fossils were not previously recognised from the Sugarloaf Creek Formation, a latest Lochkovian to earliest Pragian age assignment was made by Owen & Wyborn (1979) based on an early Pragian dating for the conformably overlying Cavan Limestone. The age of the Cavan Formation has, however, been reassessed based on conodonts (Mawson *et al.*, 1992), its lower part representing the late Pragian *pireneae* Zone. The Sugarloaf Creek Formation is thus less constrained within the Lochkovian-Pragian interval.

Maldybulakia malcolmi is common through an approximately 30 cm interval in mudstone and siltstone at an outcrop along Saltwater Creek Forest Road, near Edrom, 12 km SSE of Eden. The site (37°09'S 149°57'E) is located 3.6 km from the intersection of Saltwater Creek Road and Edrom Road in East Boyd State Forest (Fig. 1D). Fergusson *et al.* (1979: fig. 5) documented this section as examplar of lacustrine mudstones in their Facies 3 of the Boyd Volcanic Complex. They noted the occurrence of *Maldybulakia* [as "Arthropods (unidentified genus)"] with lycopods, which are abundantly represented at these levels. Some of these can be identified as *Lepidosigillaria yalwalense*, usually regarded as Middle Devonian in age (M.E. White, pers. comm., 1995). However, bothriolepid and phyllolepid placoderms indicative of a Givetian-Frasnian age are known from Facies 3 of the Boyd Volcanic Complex at other localities (Fergusson *et al.*, 1979; G.C. Young, pers. comm., 1996). The same flora occurs with late Givetian or early Frasnian fish in Facies 2 of the Boyd Volcanic Complex (Bunga Beds). On this evidence, *Maldybulakia malcolmi* can be assigned an age in the late Givetian to early Frasnian interval. The site was extensively excavated in April 1997 by the author and 11 other collectors.

Both Australian species of *Maldybulakia* are thus known from sediments deposited in fresh water, and disarticulated tergites and pleurotergites occur as rich accumulations. The geological and inferred ecological context of *M. mirabilis* in Kazakhstan is similar. The latter species occurs as abundant, mostly disarticulated, moulds in beds of tuffaceous siltstone. Tesakov & Alekseev (1992) regarded the depositional setting of these sediments as lacustrine, similar to the interpretation of mudstones bearing *M. malcolmi* (Fergusson *et al.*, 1979; P.C. Lewis *et al.*, 1994). *Maldybulakia* is, however, likely to have been terrestrial rather than aquatic, based on the inferred presence of a tracheal respiratory system (see interpretation of spiracles in *M. malcolmi* below). This in itself is not a definite indicator (aquatic insects providing an obvious exception). Comparisons with the habits of related extant arthropods are weakened by the imprecision with

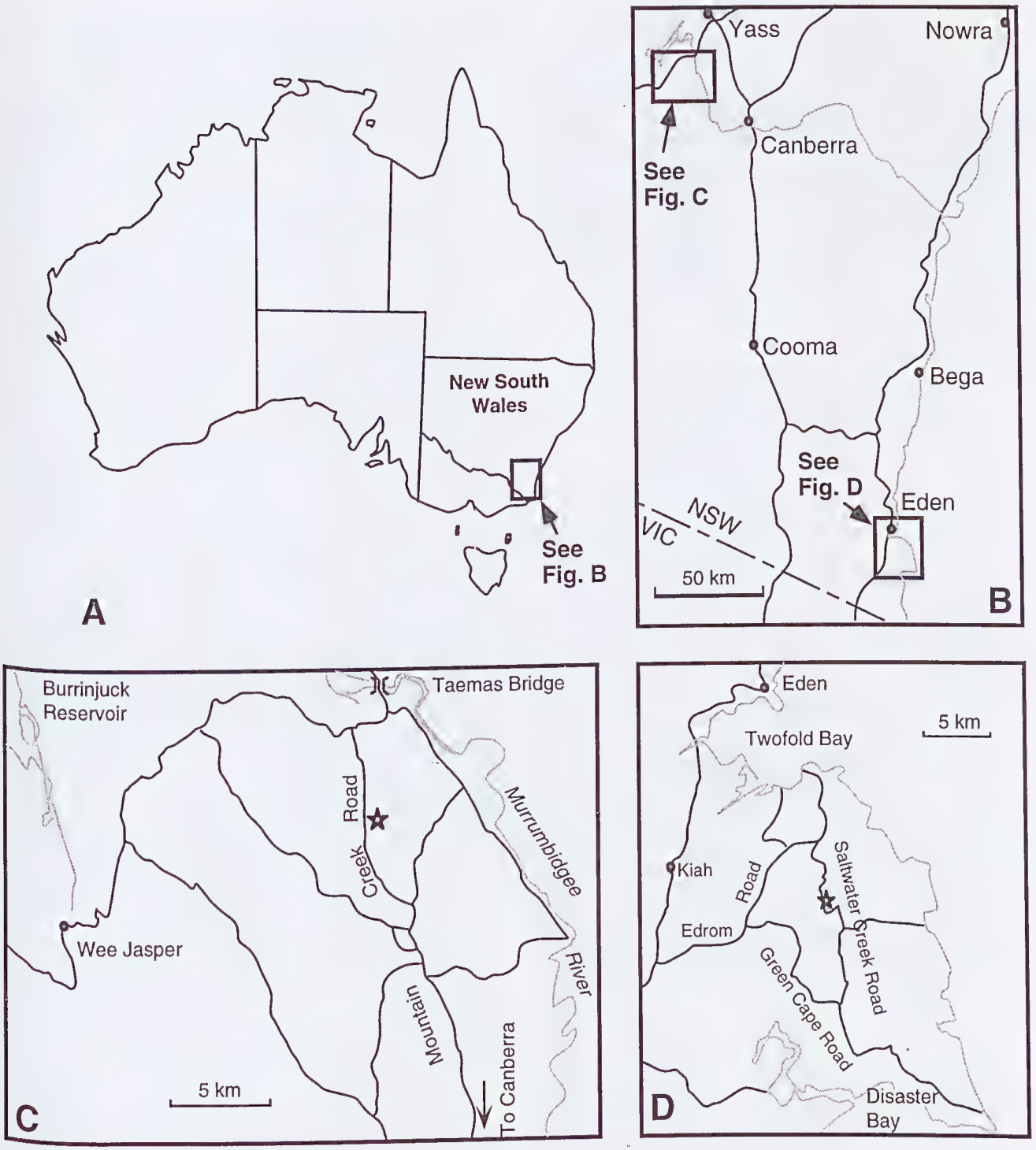

Figure 1. Occurrences of *Maldybulakia* in Australia. A, Australia, showing location of map B. B, southeastern New South Wales, with locations of maps C and D indicated by insets. C, Taemas-Wee Jasper region, with type locality of *M. angusi* indicated by star. D, Eden region, with type locality of *M. malcolmi* indicated by star.

which the affinities of *Maldybulakia* are known. In spite of this limitation, it must be observed that the myriapod affinity suggested by the apparently diplosegmental trunk (see "Phylogenetic affinities" below) leans towards a terrestrial mode of life. The only associated fossils, the abundant lycopod flora with *M. malcolmi*, are terrestrial, so the abundance of specimens in aquatic facies cannot rule out a terrestrial habitus in life. The robust construction of the exoskeleton with its strong intertergal articulations would certainly allow transport (Allison, 1986). Indeed, the concentrations of specimens and a bias towards small specimens remaining articulated, discussed below for *M. malcolmi*, are suggestive of some transport.

Systematic palaeontology

A traditional ranked classification would recognise *Maldybulakia* as distinct from other myriapodous arthropod taxa at a high level (class or subclass). As did Tesakov & Alekseev (1992), I have abstained from assigning *Maldybulakia* at most supergeneric ranks; a series of redundant, monotypic taxa does not provide insight into its systematic position. Justification for likely membership in Dignatha is presented under "Phylogenetic affinities". The taxon Myriapoda is of uncertain status (see "Phylogenetic affinities") and is not employed in this classification.

Arthropoda Siebold & Stannius, 1845

Atelocerata Heymons, 1901

?Dignatha Tiegs, 1947

Maldybulakia Tesakov & Alekseev, 1998

1992 *Lophodesmus* Tesakov & Alekseev, 1992 (non *Lophodesmus* Pocock, 1894).

Type species. *Lophodesmus mirabilis* Tesakov & Alekseev, 1992.

Diagnosis. Large myriapodous arthropod with strongly mineralised pleurotergum, unmineralised sternum; cuticular surface with dense, polygonal sculpture; cuticle densely penetrated by large pore canals; trunk composed of two tagmata of presumed diplotergites; anterior tagma of one or possibly two subtrapezoidal tergite(s) having rounded corners; posterior tagma composed of at least four pleurotergites with pair of triangular lateral lobes on metazonites and short to long paratergal spines; pleurites coalesced with metazonites only; posterior-most (fifth) bilobate tergite with median spine-like process; spiracle in pleural furrow on third pleurotergite of posterior tagma; presumed telson composed of two small sclerites.

Discussion. *Maldybulakia* Tesakov & Alekseev, 1998, was recently proposed as a replacement name for *Lophodesmus* Tesakov & Alekseev, 1992, a name occupied by the extant polydesmid millipede *Lophodesmus* Pocock, 1894. The generic diagnosis employed by Tesakov & Alekseev (1992) is modified to account for newly discovered diversity in the Devonian of Australia.

A major morphological contribution of new Australian species of *Maldybulakia* is to elucidate the nature of trunk tagmosis in this arthropod. Tesakov & Alekseev (1992) identified two tergite types in beds containing *Maldybulakia mirabilis*. The type material consists of tergites regarded by them as diplosegments, with the lateral part of the "metazonite" swollen into a rounded lobe, and a spinose projection from the lateral edge of the paratergum. This tergite type will hereafter be referred to as a bilobate pleurotergite or B-pleurotergite (specimens of *M. malcolmi* n.sp. are interpreted as having pleurites fused to the tergum, thus the use of "pleurotergites").

Associated with the B-pleurotergites is a second, less common tergite type of "simple structure and rounded-rectangular outline" (Tesakov & Alekseev, 1992: 19). Noting that the rectangular (or, more accurately, trapezoidal) tergites bore a similar sculpture to the bilobate diplotergites/B-pleurotergites, Tesakov & Alekseev (1992) acknowledged the likelihood that they could belong to the same animal. However, they interpreted the trapezoidal tergites as neck segments, but (assuming one neck segment per animal, as for the dignathan collum) found them to be anomalously common relative to the typical B-pleurotergites.

Conclusive evidence that the trapezoidal tergites (here abbreviated T-tergites) are actually part of *Maldybulakia* is provided by the Australian species, in particular by several articulated specimens of *M. malcolmi*. Four articulated specimens of *M. malcolmi* have a single T-tergite attached or slightly displaced from the front of a series of B-pleurotergites. In the holotype, a T-tergite of nearly the same size as the articulated one (width 14.4 versus 14.8 mm, respectively) is displaced 14 mm from the front of the specimen. Considering the scarcity of specimens this small it is not unlikely that the displaced tergite belongs to the same individual, which would thus possess two T-tergites. The failure to find T-tergites in articulation with each other in any specimens may derive from a mainly membranous attachment and simple overlap (in contrast to the strong articulations developed between B-pleurotergites). *Maldybulakia angusi* reveals a range of morphology within this tergite type, suggestive of two or more T-tergites represented within a tagma of generally similar tergite form. The T-tergites vary in the presence or absence of a posteromedian spine, the prominence of tubercles, the degree of sinuosity of the transverse furrow, and the presence or absence of lateral swellings. *Maldybulakia malcolmi* and *M. mirabilis* display less morphological differentiation between the tergites of this tagma than is the case for *M. angusi*. This is consistent with evidence from the tagma composed of B-pleurotergites, wherein *M. angusi* shows a much greater degree of variation than seen in the other two species.

The frequency of occurrence of the trapezoidal tergites—27 percent of the sample (N=44)—was cited by Tesakov & Alekseev (1992) as a difficulty for their interpretation of the T-tergites as neck segments. Variable frequencies of occurrence of the T- and B-tergites are observed for the two Australian species of *Maldybulakia* (Fig. 2). The relative extent of the two tagmata might be estimated by the relative abundance of T- and B-tergites, although it appears that taphonomic factors have biased the samples. Three articulated specimens of *M. malcolmi* (AM F.102533, 102535, 102357) have a single T-tergite followed by four B-pleurotergites, then a caudal tergite as figured for *M. mirabilis* by Tesakov & Alekseev (1992). The caudal tergite is quite clearly a modified B-pleurotergite, showing the rounded lateral lobes and depressed, anterior overlapped surface (prozonite) typical

of those pleurotergites. This serial homology is also obvious in *M. malcolmi*, in which the caudal tergite possesses small posterolateral projections as in the B-pleurotergites.

For *Maldybulakia angusi*, a survey of 301 sclerites that could be confidently identified.as either a T-tergite, ring tergite, B-pleurotergite or caudal tergite shows that T-tergites comprise 32 percent of the sample and B-pleurotergites 66 percent (Fig. 2c). It might thus be inferred that the anterior tagmata composed of T-tergites is half the length of the tagmata comprising B-pleurotergites, which would accord well with the two T-tergites and four B-pleurotergites seen in the holotype of *M. malcolmi*. A ring-like tergite that overlies the prozonite of the anteriormost B-pleurotergite (and has processes permitting articulation of the T-tergite) in *M. malcolmi* is represented by only 4 of 301 specimens of *M. angusi* and is unreported in the sample of *M. mirabilis* (Fig. 2d). Given that each individual possesses one of this sclerite type it is underrepresented in the sample. Caudal tergites are significantly underrepresented, known from only two specimens.

The relative abundance of disarticulated tergites in *M. malcolmi* differs from the 2:1 ratio of B:T tergites in the sample of *M. angusi* as well as the 4:1 or 4:2 ratio predicted by articulated specimens (Fig. 2a,b). Of disarticulated tergites of *M. malcolmi*, 185 are B-pleurotergites (83 percent) and 28 are T-tergites (12.6 percent). The apparent over-abundance of B-tergites is at the expense of ring tergites (3.1 percent) and caudal tergites (1.3 percent). These differences between the three species, if not entirely due to differential transport of the various sclerite types, might result from a greater number of T-tergites in *M. angusi* compared to *M. malcolmi*. There is a significant taphonomic bias observed in the case of articulation. Articulated specimens of *M. malcolmi* are smaller than most of the disarticulated material, presumably because larger specimens did not survive transport intact.

Although the trunk of *Maldybulakia angusi* displays much more serial variation than that of *M. malcolmi*, it has proven possible to identify most tergites of the former according to their position in the latter, and it cannot be ruled out that *M. angusi* may possess the same number of tergites in the trunk as known for *M. malcolmi* (one or possibly two T-tergites, a ring tergite, four B-pleurotergites and a caudal tergite). The minimal number of tergites in *M. angusi* is discussed more fully after description of that species.

Tesakov & Alekseev's (1992) evidence for regarding the B-pleurotergites of *Maldybulakia mirabilis* as diplosegmental (diplotergites) was their "distinct two-part structure". This refers to the separation of the anterior, articulating surface of the tergite from the posterior lobate part by a strong transverse groove or stricture. The T-tergites are of comparable proportions (length versus width) to the B-pleurotergites, and are also divided lengthwise by a transverse furrow in Australian species of *Maldybulakia*. This would suggest that they, too, would be diplotergites if the posterior trunk tergites were confirmed as being diplosegmental. All of the Palaeozoic myriapodous arthropods that might be compared with *Maldybulakia* on the basis of tergite form have proven to be diplosegmental when the appendages became known. Examples are kampecarids (Almond, 1986), euphoberiid millipedes (Burke, 1979), and arthropleurids (Briggs & Almond, 1994). It is thus likely that the trunk tagmata of *Maldybulakia* are composed of diplosegments. The strong intertergal articulations and overlap of the prozonite of the B-pleurotergites by the preceding metazonite suggest that *Maldybulakia* had the capacity to enroll.

A pair of articulated sclerites are preserved just behind the caudal pleurotergite of the holotype of *Maldybulakia malcolmi* (Fig. 3a,g). They are also known from disarticulated specimens (Fig. 4g). Their positioning on the articulated specimen is a strong indication that they represent the posterior sclerites, although the nature of their (presumed) articulation to the caudal pleurotergite is not understood. Their small size, inferred posterior position, and overall structure invite a comparison with the telson of myriapods, which may also incorporate multiple sclerites (e.g., preanal sclerite or preanal ring, anal valves, and subanal plate in diplopods; Enghoff, 1990: 14–15). In the descriptions below, these two sclerites are called telson sclerites.

Information on pleural morphology is supplied by *Maldybulakia malcolmi*. The lateral exoskeletal component of *Maldybulakia* is regarded as a mineralised part of the pleuron (i.e., pleurites), rather than the tergum (paratergites) because of its marked topographic separation from the tergum. Alternative interpretations of pleural structures are addressed under discussion of *M. malcolmi*.

The lack of sampling of a head in the Australian occurrences is curious, given the abundance of trunk tergites known for both species. Almond (1986) observed that articulated heads were rare in the possibly allied kampecarids, even when the trunk was fully articulated, and attributed this to a delicate attachment by arthrodial membrane, as is the case in millipedes. The head tergite of *Kampecaris* is a rather featureless plate (or pair of plates, the second possibly a collum according to Almond, 1986). The narrow sclerite alleged to be the head of *Arthropleura* (Briggs & Almond, 1994: figs. 1, 2; Brauckmann *et al.*, 1997) requires confirmation, as it may instead represent a collum-like tergite (W.A. Shear & H. Winkelmann, pers. comm., 1997). Even if the head of *Maldybulakia* likewise involved a simple plate it is unlikely that it has been overlooked because sclerites of this sort were deliberately sought, yet no candidates have appeared. Heads likely underwent a different transport history than the trunk, perhaps because of a membranous attachment. The possibility that specimens such as the holotype of *M. malcolmi* are complete, with the T-tergite being cephalic, is not favoured. This sclerite deviates from an expected morphology of an arthropod cephalon (e.g., lacking eyes or structures to accommodate them; lacking antennal sockets or notches), its transverse stricture and shape of the doublure conforming to a trunk diplotergite. The abrupt anterior termination of the doublure (Fig. 6b) indicates a more anterior sclerite. The possibility that a species may possess two of these tergites further weakens the case for

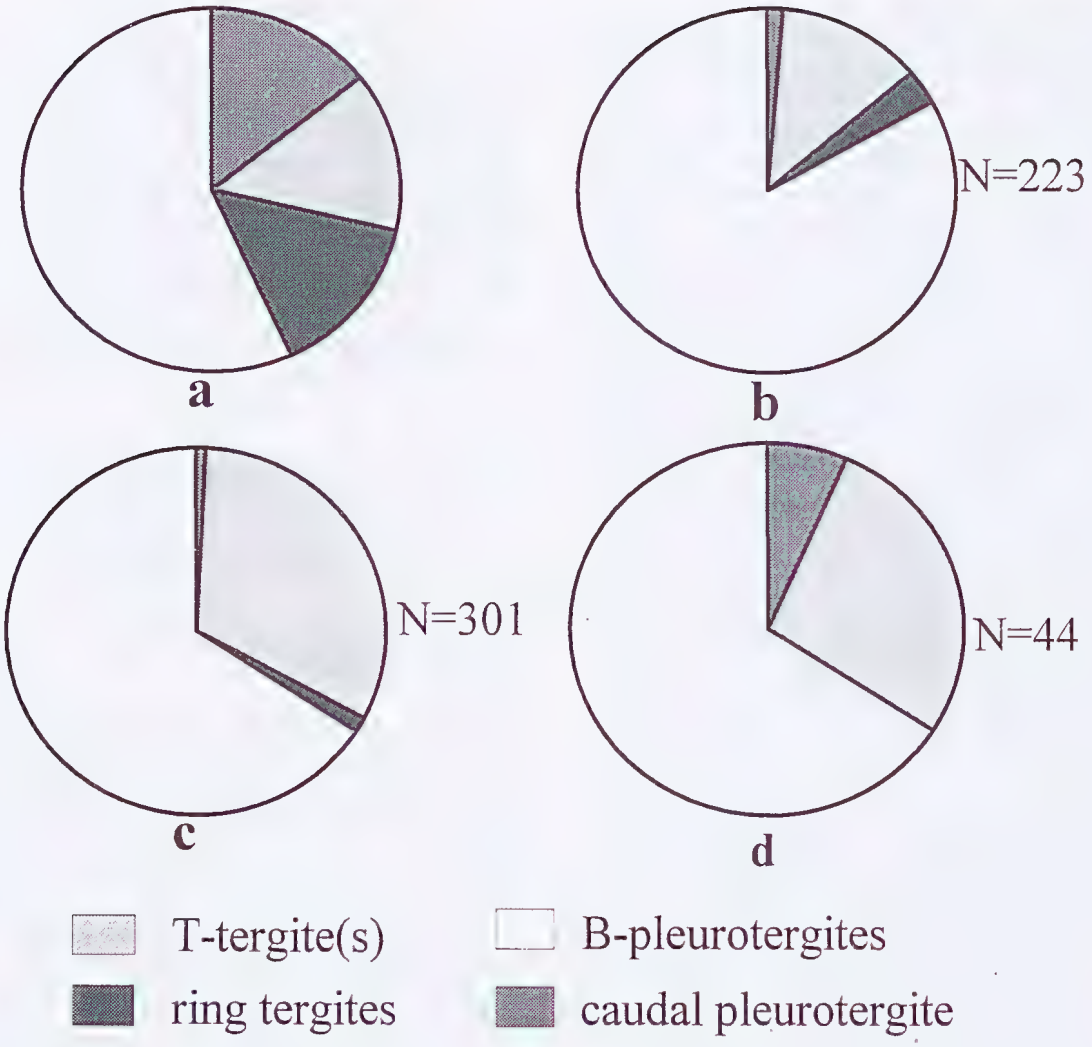

Figure 2. Relative abundances of different sclerite types at localities yielding *Maldybulakia*. (*a*) expected frequency of occurrence for *M. malcolmi* n.sp. based on one T-tergite, one ring tergite, four B-pleurotergites, and one caudal pleurotergite in articulated specimens. (*b*) sampled frequency of occurrence based on 223 disarticulated sclerites of *M. malcolmi*. (*c*) sampled frequency of occurrence based on 301 disarticulated sclerites of *M. angusi* n.sp. (*d*) sampled frequency of occurrence based on 44 disarticulated sclerites of *M. mirabilis* (Tesakov & Alekseev, 1992).

a cephalic identity. All of these factors outweigh the crude similarities in outline between a T-tergite and some arthropod head shields (e.g., the prosoma of bunodid xiphosurids, which has typical cephalic structures such as a cardiac lobe and ophthalmic ridges that are lacking in *Maldybulakia*).

A few disarticulated sclerites do not conform to those in articulated specimens of *Maldybulakia malcolmi*, and their position in the exoskeleton is unknown. A unique specimen of *M. malcolmi* (Fig. 5g,h) has a prominent, square embayment in could be presumed to be the posterior margin (this assuming that the strongly convex, ridge-like edge of the specimen is overlapped in articulation, as is the case for the prozonites). The conical median swelling warrants comparison with the caudal pleurotergite, although this swelling is strongly dorsally directed. The size and shape of the embayment invite speculation that the telson sclerites (Fig. 4g) might attach here. However, it does not seem possible that such a large, robust sclerite could be positioned posteriorly in the trunk yet be missing from the holotype and other articulated specimens. As such, it is more likely situated anterior to the T-tergites, but attempts to interpret it as a head are unconvincing, lacking any landmarks indicative of an arthropod cephalic shield or head capsule.

Maldybulakia malcolmi n.sp.

Figs. 3–8

Maldybulakia new species 1 Edgecombe, 1998: fig. 1.

Etymology. For Malcolm Young.

Diagnosis. *Maldybulakia* with relatively minor serial variation in B-pleurotergites; lacking long paratergal spines, posteromedian spines, and tuberculation; caudal pleurotergite with lateral lobes set off by shallow furrows; median projection on caudal pleurotergite blunt, conical, rather than spinose.

Types. HOLOTYPE articulated trunk AM F.102533 (Fig. 3a–d,f,g), composed of one T-tergite, four B-pleurotergites, a caudal tergite, disarticulated telson sclerites; and possibly associated T-tergite; length from anterior end of T-tergite to posterior end of caudal pleurotergite 31.8 mm. Boyd Volcanic Complex (late Givetian or early Frasnian), Saltwater Creek Road, East Boyd State Forest, NSW (37°09'S 149°57'E). Collected by Z. Johanson. PARATYPES AM F.102534–102556, 102581, from type locality.

Description. Trunk up to 115 mm long, as inferred from size of largest known B-pleurotergite scaled to articulated specimen.

T-tergite(s) of length up to 16.4 mm in known specimens, but inferred to be larger based on relative size of B-pleurotergites; smallest disarticulated specimen 5.1 mm long medially. Length 38–44 percent of width; of even, moderate convexity (tr.). Anterior part of prozonite a forward-sloping scarp that evenly lengthens medially to about 45 percent the length of the prozonite. Stricture moderately deep and approximately transverse medially, then weakly curving backwards laterally, abruptly shallowing and recurving forward, then inward, such that lateral part of stricture is C-shaped. Metazonite 64–75 percent length (sag.) of prozonite; gently convex (sag.). Lobate posterior projections lie against anterodistal socket-like processes on underlying ring tergite, serving as point of articulation. Posterior margin gently convex forwards between posterior projections. Doublure wide beneath lateral and posterolateral edges of T-tergite, shortening and scalloped on each side of a flange-like median section that has a transverse course; doublure abruptly truncated anteriorly, with straight anteromedial margin.

Ring tergite (Fig. 5b,d–f) divided by sharp transverse furrow into short, crest-like anterior band of even length and long, elevated posterior band; furrow strongly shallow or effaced near distal margin. Anterior band extended laterally well outside posterior band as slender, pointed process; anterodistal edge folded as a small socket-like process. Posterior band lenticular in outline, convex (sag.), moderately arched transversely. Ring tergite overlapping prozonite of first B-pleurotergite, with distal edge of posterior band extending to inner edge of anterior process on prozonite of B-pleurotergite.

Posterior tagma composed of four B-pleurotergites and caudal pleurotergite, widest across first pleurotergite then gently, evening narrowing posteriorly; largest known disarticulated specimen (second B-pleurotergite) of length 25.8 mm, width 45 mm; smallest disarticulated specimen (fourth B-pleurotergite) 7.5 mm long, but as short as 6 mm in articulated specimens. Relative length and width of pleurotergites variable (compare Figs. 3a and 5i for relatively narrow and wide examples, respectively); each pleurotergite longer relative to its width than the preceding one. Furrows separating prozonite and metazonite on all four pleurotergites of similar, moderate depth, long medially, narrower but with comparable depth against lateral lobes. In sagittal profile, prozonites gently convex, metazonites flat or weakly convex along most of length; median lobe raised well above lateral lobes. Lateral lobes of all four pleurotergites triangular, with short, blunt posterolateral projections, in some specimens developed as weak spines. Metazonites progressively more strongly arched (tr.) posteriorly in trunk. Diagonal furrows separating lateral and median lobes of equal impression on each B-pleurotergite, gently convex backward.

First B-pleurotergite (Figs. 3e, 6c–e) with outer margin of lateral lobe oriented posterolaterally in dorsal view, gently convex outward, this margin posteriorly directed on the succeeding three pleurotergites with a corresponding posterior redirection of the posterolateral projections. Prozonite lenticular, with a strong process at anterodistal edge that is lacking on succeeding pleurotergites. Lateral edge of tergum sharply folded down as vertical scarp; lenticular pleurite separated by sharp, curved pleural furrow; pleural furrow effaced posteriorly; separation of pleuron and tergum not marked by suture on posterior part of pleurotergite; posteroventral edge of pleurotergite turned out as a rounded shelf.

Second B-pleurotergite (Fig. 6g–j) having anteroventral edge of prozonite forming a narrow, steep rim; anterolateral corner of tergite with ledge-like protrusion markedly distal to pleuron; small ventrally directed pleural process at anterior corner of metazonite, ventral margin of pleuron abruptly flexed ventrally immediately behind this process; pleuron bisected by anterodorsally oriented groove; posterior part of pleuron lensoid in outline, gently sloping outward; pleural furrow indistinct on posterior part of pleurotergite.

Third B-pleurotergite (Fig. 3b,c,f) with pleural furrow expanded anteriorly to form a shallow, elongate basin within which a deep, elliptical canal (spiracle) projects inwards; pleurite narrow beneath spiracular region, then abruptly widening; rounded ventral projection on anterior part of pleurite as on preceding diplopleurotergite; sharp, shallow suture between pleurite and pleural furrow anteriorly.

Fourth B-pleurotergite with lateral lobes of metazonite terminating as posteriorly-directed angulations. Weak nodose swelling usually distinguishable on posteromedian part of median lobe of metazonite (Figs. 3a, 5k), occasionally discernible on other B-pleurotergites. Pleural furrow deep, incised as a V-shaped groove along most of

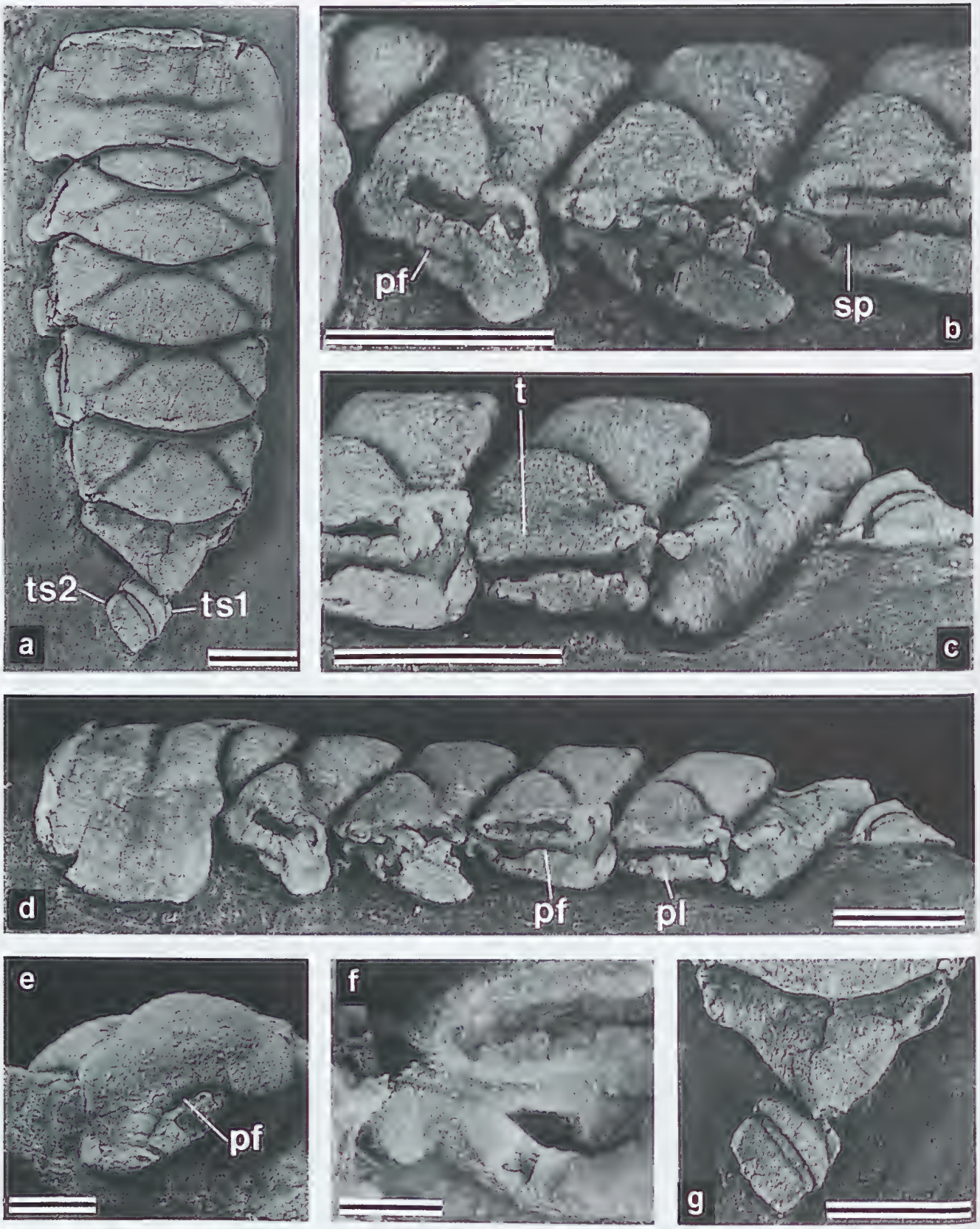

Figure 3. *Maldybulakia malcolmi* n.sp. Scale bars 5 mm except *f*, 1 mm. Abbreviations: pf, pleural furrow; pl, pleurite; sp, spiracle; t, lateral edge of tergum; ts1, anterior telson sclerite; ts2, posterior telson sclerite. (*a–d,f,g*) holotype articulated trunk AM F.102533. (*a*) dorsal view of complete specimen. (*b,c*) lateral views of anterior and posterior B-pleurotergites, respectively. (*d*) lateral view of complete specimen. (*f*) lateral view of third B-pleurotergite with spiracle. (*g*) dorsal view of caudal pleurotergite and telson sclerites. (*e*) posterolateral view of first B-pleurotergite AM F.102552 (see Fig. 6d for dorsal view), showing pleural furrow (pf).

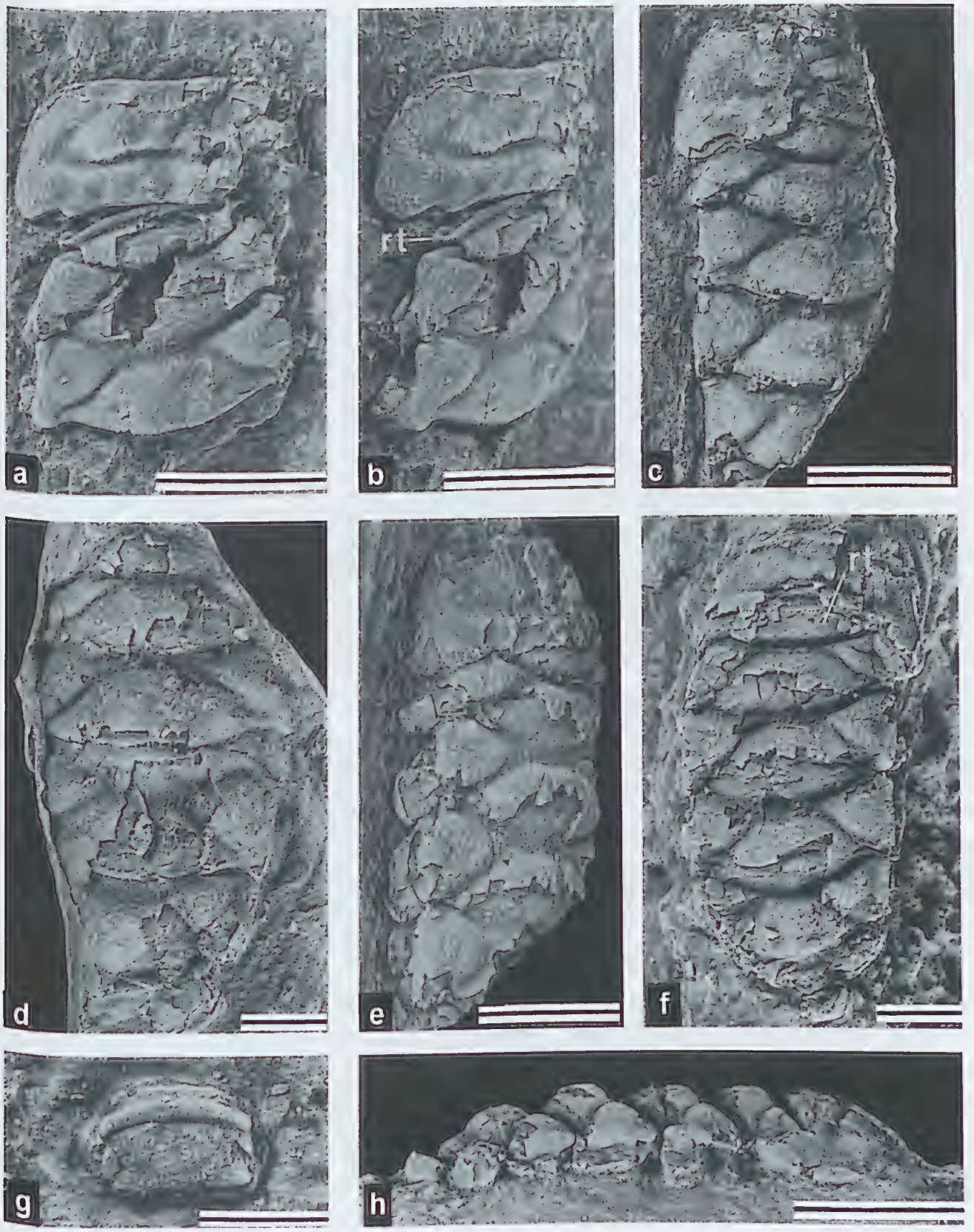

Figure 4. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm except *d,f,g*, 5 mm. (*a,b*) dorsal and left dorsolateral views of T-tergite, ring tergite, and first two B-pleurotergites, AM F.102534. (*c*) dorsal view of latex cast of articulated trunk AM F.102535a, showing T-tergite, ring tergite, four B-pleurotergites and part of caudal pleurotergite. (*d*), dorsal view of latex cast of ring tergite and four B-pleurotergites, AM F.102536. (*e*) left dorsolateral view of trunk AM F.102535b (see Fig. 4c for counterpart). (*f,h*) dorsal and right lateral views of articulated trunk AM F.102537, showing posterior part of T-tergite, ring tergite (rt), four T-pleurotergites, and part of caudal pleurotergite. (*g*) dorsal view of telson sclerites AM F.102538.

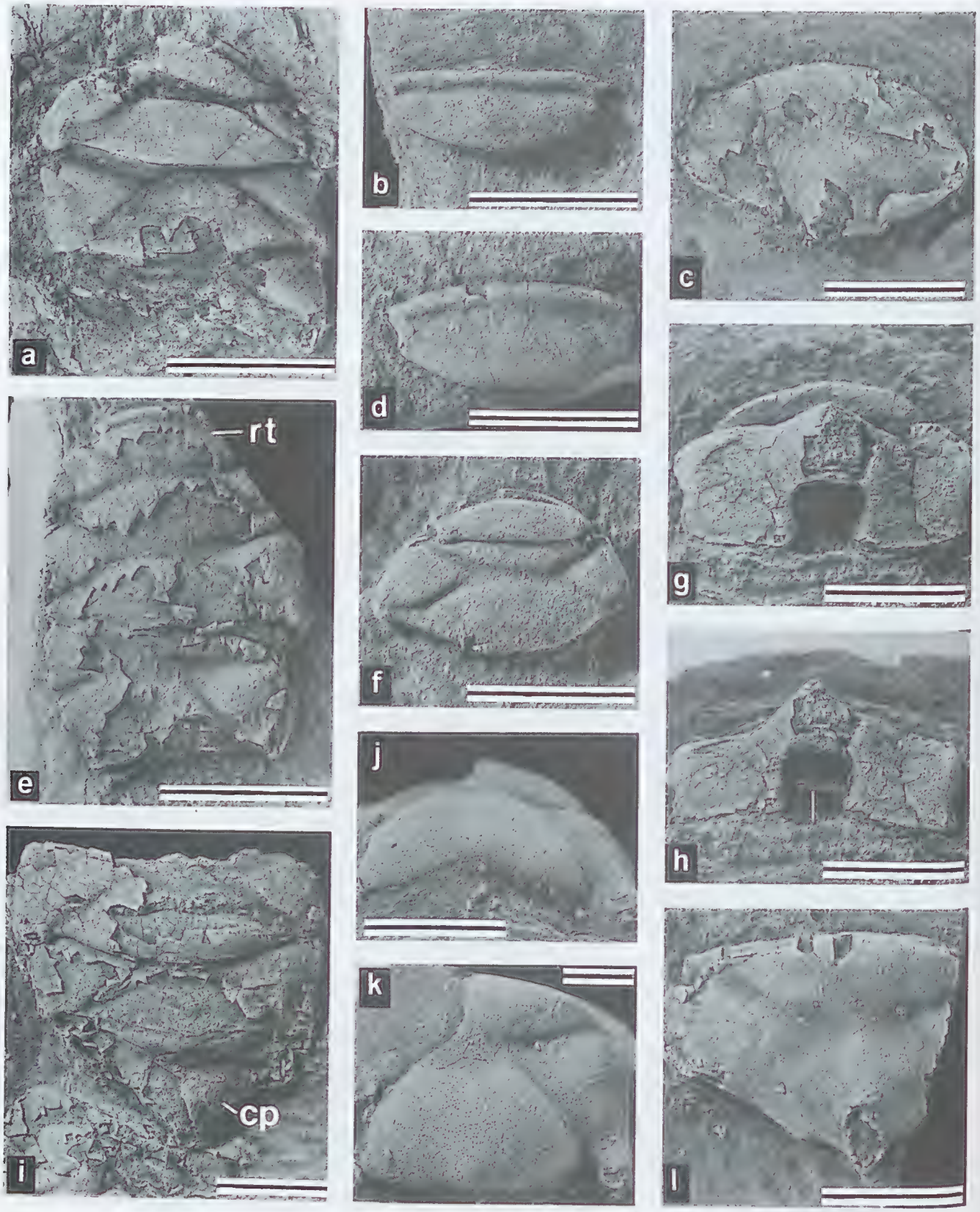

Figure 5. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm except *k*, 5 mm. (*a*) dorsal view of ring tergite and three B-pleurotergites, AM F.102539. (*b*) dorsal view of ring tergite AM F.102540. (*c*) dorsal view of caudal pleurotergite, AM F.102541. The median swelling in this specimen is more dorsally directed than in other specimens. (*d*) dorsal view of ring tergite AM F.102542. (*e*) dorsal view of ring tergite (rt) and three B-pleurotergites, AM F.102543. (*f*) dorsal view of ring tergite and first B-pleurotergite, AM F.102544. (*g,h*) dorsal and anterior or posterior view of unique sclerite of unknown position, AM F.102545. White line in *h* indicates limit of exoskeleton in the embayment. (*i*) dorsal view of posterior two B-pleurotergites and caudal pleurotergite (cp), AM F.102546. (*j,k*) posterior and dorsal views of fourth B-pleurotergite, AM F.102547. (*l*) dorsal view of caudal pleurotergite AM F.102548.

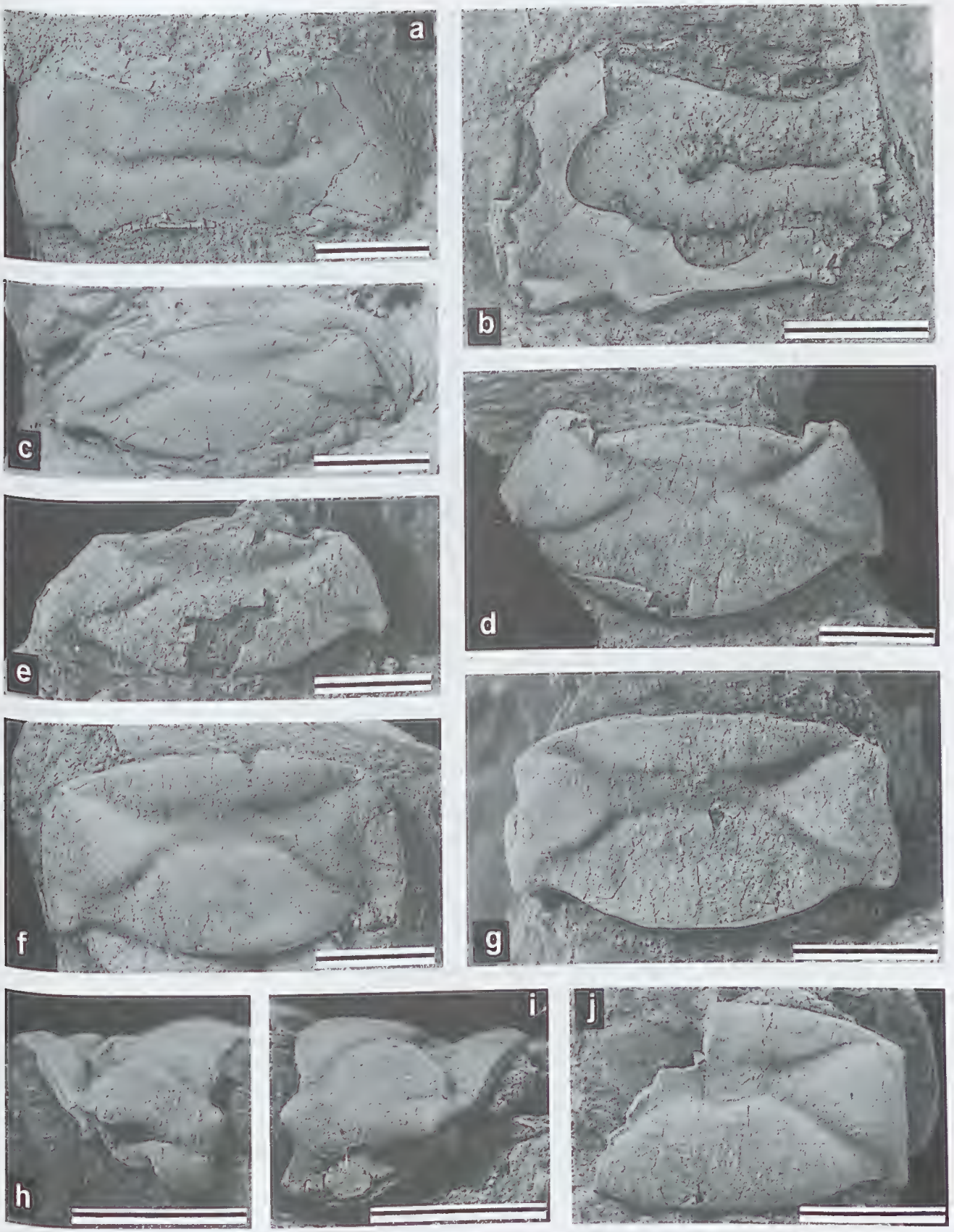

Figure 6. *Maldybulakia malcolmi* n.sp. Scale bars 10 mm. (*a*) dorsal view of T-tergite AM F.102549. (*b*) ventral view of T-tergite AM F.102550, showing doublure. (*c*) dorsal view of first B-pleurotergite AM F.102551. (*d*) dorsal view of first B-pleurotergite AM F.102552. (*e*) dorsal view of first B-pleurotergite AM F.102553. (*f*) dorsal view of B-pleurotergite AM F.102554. (*g,h*) dorsal and left lateral views of second B-pleurotergite AM F.102555. (*i,j*) right lateral and dorsal views of second B-pleurotergite AM F.102556.

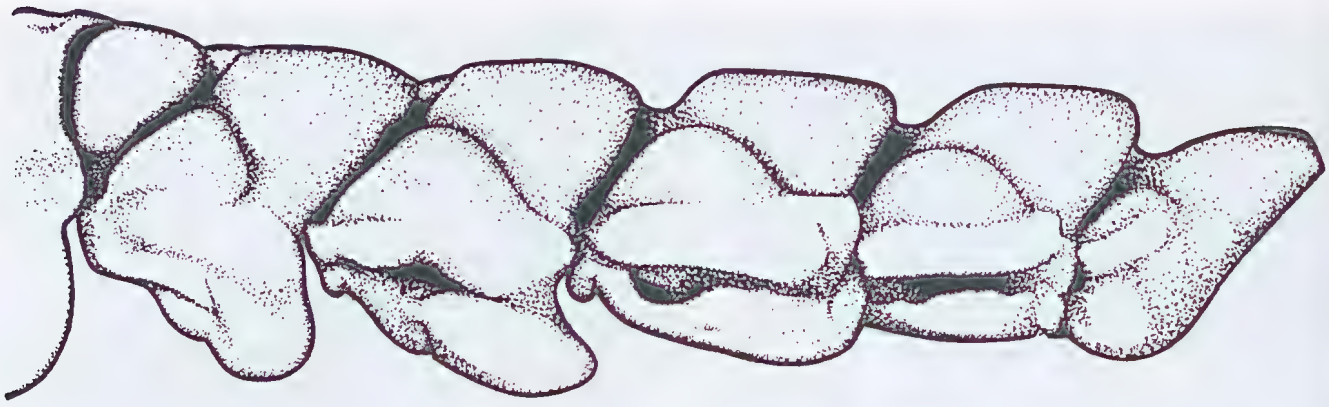

Figure 7. *Maldybulakia malcolmi* n.sp. Reconstruction of trunk in lateral view, showing serial variation in structures of the pleurotergum. Based mostly on AM F.102533 (Fig. 3*b–d*).

juncture between tergum and pleuron, abruptly shallowing near posterior margin. Pleurite clavate, narrowest anteriorly, projecting only slightly outside lateral edge of tergum.

Caudal tergite (Figs. 3c,g, 5i,l) with prozonite longer than on preceding B-pleurotergites, weakly convex (sag.); furrow between prozonite and metazonite shallow medially, distinctly deeper against lateral lobes; lateral lobes flat, set off by weak furrow; lateral edge of tergum forming a slender ridge that gently bulges beyond otherwise triangular outline of metazonite in dorsal view; pleural furrow not impressed; posteromedian process large, conical, triangular or elliptical in section posteriorly, gently turned up; posterolateral margin vertically inclined, gently convex.

Two small telson sclerites (Figs. 3g, 4g). Anterior telson sclerite divided into a depressed anterior band that resembles an articulating edge and a longer, convex, strongly arched (tr.), posterior band; about 40 percent width of caudal pleurotergite. Posterior telson sclerite divided by a sharp transverse furrow into short anterior band and flattened, broadly quadrate posterior plate; anterior band overlapped by anterior telson sclerite.

Dorsal surface of cuticle densely covered with honeycomb-like, shallow, polygonal pits; density of polygons the same on prozonite, stricture, and metazonite. Cuticle replaced with chalcedony, divided into a thin outer layer (0.04 mm) and thicker main layer (0.45 mm), measured in thin section; internal fabric of main layer obliterated by chalcedony aggregates. Large, densely arranged canals run through cuticle perpendicular to its surface (Fig. 8a), opening to variable-sized, rounded pits on ventral surface (Fig. 8b).

Discussion. The description of this species regards the trunk as being composed of pleurotergites, the pleurites being fused to the tergal metazonites (Fig. 7). The two components are set off by a deep groove, described as a pleural furrow. That the pleuron is actually fused to the tergum is most evident in the posterior part of the first (Fig. 3b,e) and second (Fig. 6i) pleurotergites, where they are in direct continuity, the first pleurotergite without even a trace of a suture behind the abruptly-effaced pleural furrow. The morphology of the pleuron is frequently complicated by crushing, on occasion giving the appearance of several pleurites. In the holotype in particular, this appearance is compounded by fracture along the lateral edge of the tergum on the first three pleurotergites (Fig. 3b–d). Comparison with other specimens (Figs. 3e, 6h,i) which have an intact down-folded edge of the tergum clarifies the structures (Fig. 7). Every B-pleurotergite (even disarticulated ones) preserves the pleuron in association with the tergites, and they have characteristic morphologies on each of the four B-pleurotergites. Were the pleurites separate, unfused elements (e.g., as in centipedes) this invariant association with the tergum would not be maintained. Whether the pleural component of the pleurotergum may consist of multiple, fused pleurites is not certain. In at least some pleurotergites (Fig. 3c, particularly the fourth B-pleurotergite) the pleuron consists of a simple, elongate band without sutures, and seems likely to be composed of a single pleurite.

Serial variation in the B-pleurotergite series includes a progressive decrease in the height of the lateral edge of the tergum, and an increase in the length of the pleural furrow (short on the first B-pleurotergite versus the entire length of the fourth B-pleurotergite). The pit interpreted as a spiracle is present on a single pleurotergite, and is only distinguishable on the holotype (Fig. 3b,f). This opening is not a preservational artifact because it is entirely lined with cuticle, forming a distinct, ovate canal. The position of such a canal at the juncture between the tergum and pleuron resembles that of some tracheates (e.g., pleurostigmophoran chilopods, hexapods). The existence of only one such opening, rather than a series along the trunk, does not negate identity as a spiracle, although it is peculiar given the substantial size of *Maldybulakia*; presence of only one or two spiracles in extant myriapods (e.g., Symphyla and some lithobiomorphs) is reasonably regarded as linked to minute body size. To consider alternative interpretations, the tube in *Maldybulakia* is situated in the appropriate position for an ozopore, the

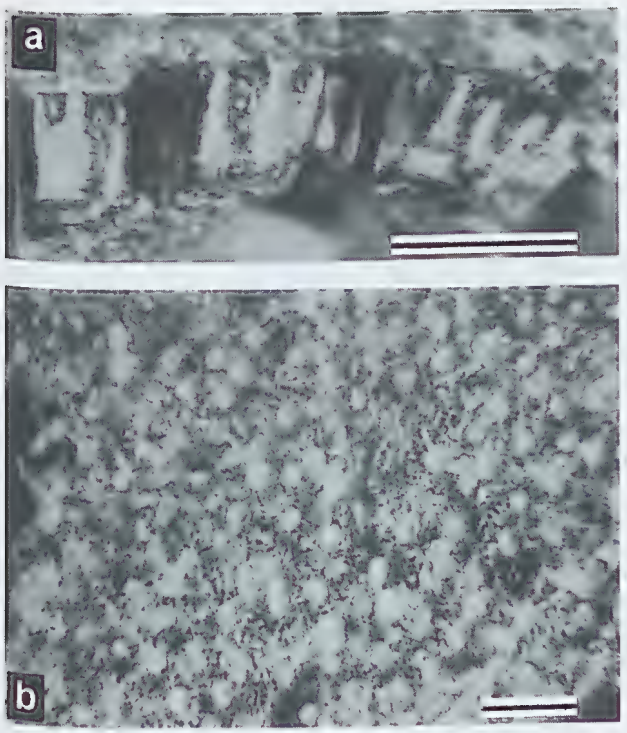

Figure 8. *Maldybulakia malcolmi* n.sp. Scale bars 1 mm. (*a,b*) T-tergite AM F.102581. (*a*) dorsoventral section through exoskeleton on lateral part of metazonite, ventral surface down, anterior to left, showing large canals filled with clay and silt matrix (light colour, versus darker exoskeleton). (*b*) ventral surface of exoskeleton on lateral part of metazonite, showing openings of canals as large, round pores filled with light-coloured matrix.

opening for the repugnatorial glands in helminthomorph diplopods (see Shear, 1993: fig. 2 for a fossil example). Such an identity is considered less likely than a spiracle because an ozopore would be expected to be smaller, whereas myriapod spiracles can be very large (e.g., in scolopendrid chilopods; see J.G.E. Lewis *et al.*, 1996).

A lesser degree of serial variation within the two trunk tagmata is a character uniting *Maldybulakia malcolmi* and *M. mirabilis* to the exclusion of *M. angusi*. Suppressed variation is, however, presumed to be a primitive condition (with outgroup comparison to other myriapods), and not indicative of a sister species relationship between *M. malcolmi* and *M. mirabilis*. Given that *M. malcolmi* has only four B-pleurotergites (not counting the caudal pleurotergite), it is likely that the four articulated B-pleurotergites in the holotype of the very similar *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1a,b) represent the entire B-pleurotergite series. *Maldybulakia malcolmi* is distinguished from *M. mirabilis* by its pronounced transverse furrow on the T-tergite (as opposed to a pair of chevron-shaped, longitudinally aligned furrows in *M. mirabilis*), much finer granulation on the tergites, shallow (versus deep) furrows setting off the lateral lobes on the caudal pleurotergite, and a less spinose median projection on that sclerite.

Maldybulakia angusi n.sp.

Figs. 9–12

Maldybulakia new species 2 Edgecombe, 1998: fig. 2.

Etymology. For Angus Young.

Diagnosis. *Maldybulakia* with considerable serial variation in B-pleurotergites; posteromedian spine present on some tergites of anterior and posterior trunk tagmata; very long, posterolaterally-directed paratergal spines on most bilobate trunk pleurotergites; caudal tergite bearing long median spine; many tergites bearing robust tuberculation.

Types. HOLOTYPE trunk pleurotergite (B-pleurotergite) AM F.102565 (Fig. 10a); length 24.6 mm. Sugarloaf Creek Formation (Lochkovian or Pragian), near Three Oaks, Taemas district, New South Wales (35°04'S 148°51'E). PARATYPES AM F.102557–102564, 102566–102580, from type locality.

Description. T-tergites (Fig. 9a–h) with length 32–39 percent of width. Anterior part of prozonite a flattened, boomerang-shaped surface that slopes forwards and lengthens medially to about 50 percent the length of the prozonite; rear edge of this surface forms a crest-like rise above posterior part of prozonite; well preserved specimens show dense, scaly sculpture (Fig. 9c). Posterior part of prozonite with pair of moderately wide longitudinal furrows varying from faint to distinctly incised. Stricture moderately deep, gently convex forward medially, recurved distally around elliptical or teardrop shaped lateral lobes. Metazonite 70–86 percent length of prozonite. Posteromedian spine absent or short. Posterior margin approximately transverse between lobate processes which vary from broad and rounded to angular to short, slender spines. Tuberculation usually strong, rarely faint, sometimes more prominent on prozonite than on metazonite. Doublure (Fig. 9a) as described for *M. malcolmi*.

Ring tergite (Fig. 9i) as for *M. malcolmi*.

B-pleurotergites up to 24.6 mm in length. Anteriormost B-pleurotergite (Fig. 10b,f,h,i) distinguished by relatively short, wide proportions and short, knob-like projections at anterolateral edge of prozonite as seen in this pleurotergite only in *M. malcolmi*. Prozonite about 25 percent length of tergite, with cuticular sculpture of dense polygonal depressions amidst a network of low ridges (Fig. 10i). Lateral lobes of metazonite teardrop shaped, outer margin rounded, strongly inflated, with steep lateral and anterior edges encircled by well-impressed furrow. Posteromedian spine on median lobe of metazonite short, conical, and posterodorsally directed or absent. Paratergal spines long, strongly divergent (directed back 40–50 degrees from transverse line), largest known specimen 88 mm wide across spines (extrapolated from one half); inferred width across spines up to approximately 115 mm (based on size relative to largest known B-pleurotergites); dorsal and

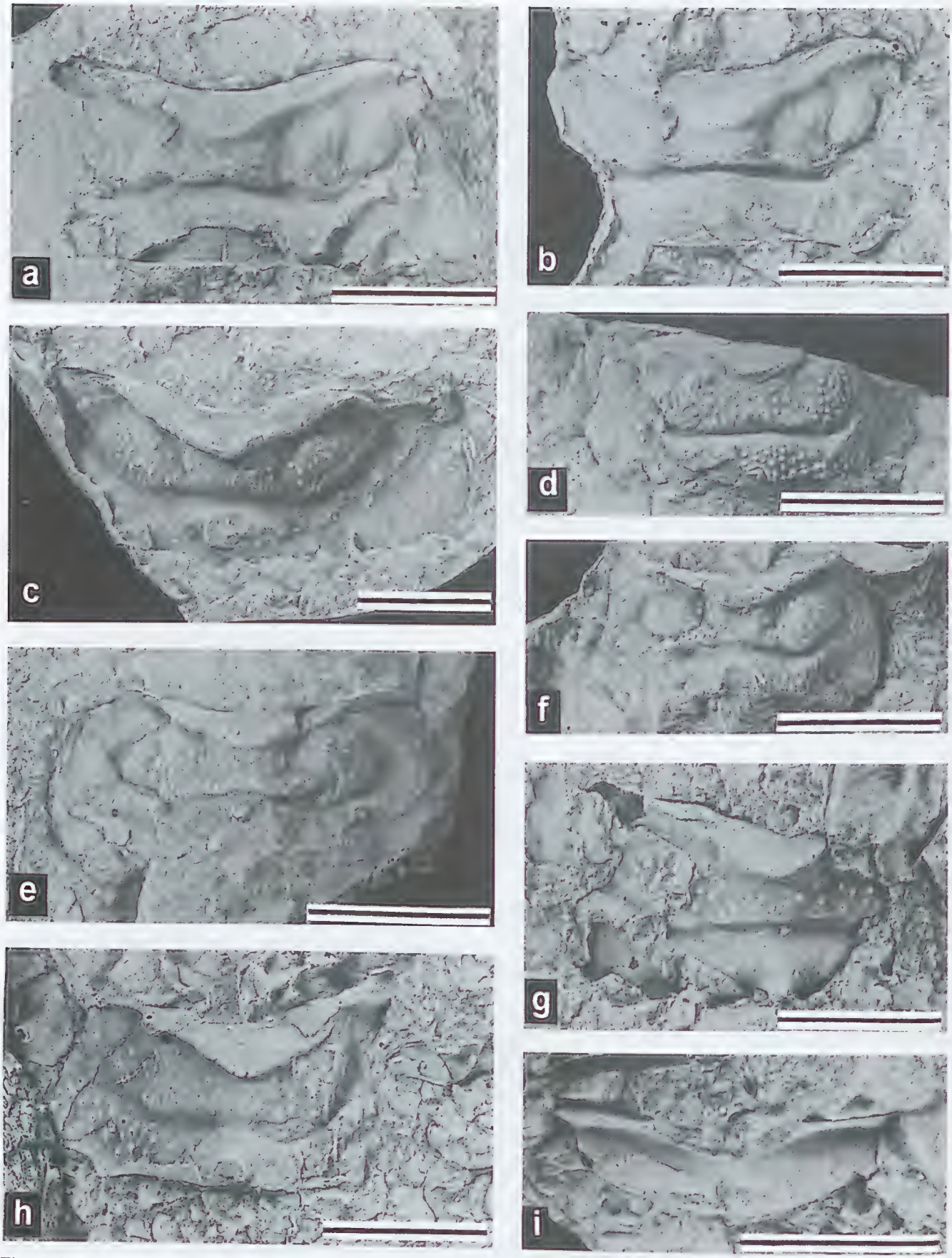

Figure 9. *Maldybulakia angusi* n.sp. Scale bars 10 mm. Latex casts from external moulds except *a, d, e, i*, internal moulds. (*a,b*) dorsal views of T-tergite AM F.102557b and AM F.102557a. Note doublure in *a*, with median flange and expanded posterolateral portion. (*c*) dorsal view of T-tergite AM F.102558. (*d*) dorsal view of T-tergite AM F.102559. (*e*) dorsal view of T-tergite AM F.102560. (*f*) dorsal view of T-tergite AM F.102561. (*g*) dorsal view of T-tergite AM F.102562. (*h*) dorsal view of T-tergite AM F.102563. (*i*) anterodorsal view of ring tergite AM F.102564.

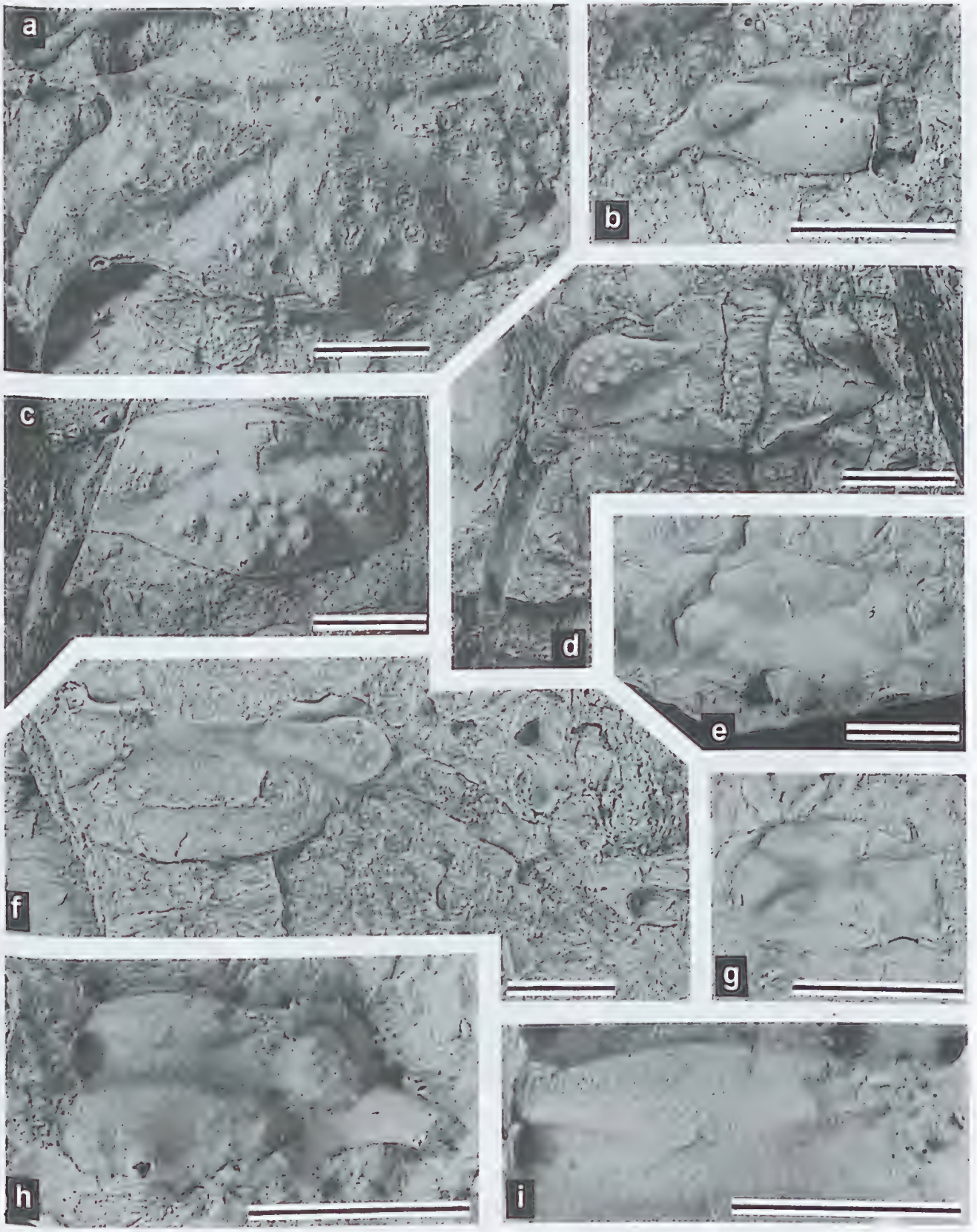

Figure 10. *Maldybulakia angusi* n.sp. Scale bars 10 mm, except *b*, 5 mm. Latex casts from external moulds except *d*, *f*, *g*, internal moulds. (*a*) dorsal view of holotype B-pleurotergite AM F.102565. (*b*) dorsal view of first B-pleurotergite AM F.102566. (*c*) dorsal view of B-pleurotergite AM F.102567. (*d*) dorsal view of B-pleurotergite AM F.102568. (*e*) dorsal view of B-pleurotergite AM F.102569. (*f*) dorsal view of first B-pleurotergite AM F.102570. (*g*) dorsal view of B-pleurotergite AM F.102571. (*h,i*) dorsal views of first B-pleurotergite AM F.102572. (*i*) detail showing polygonal sculpture on prozonite.

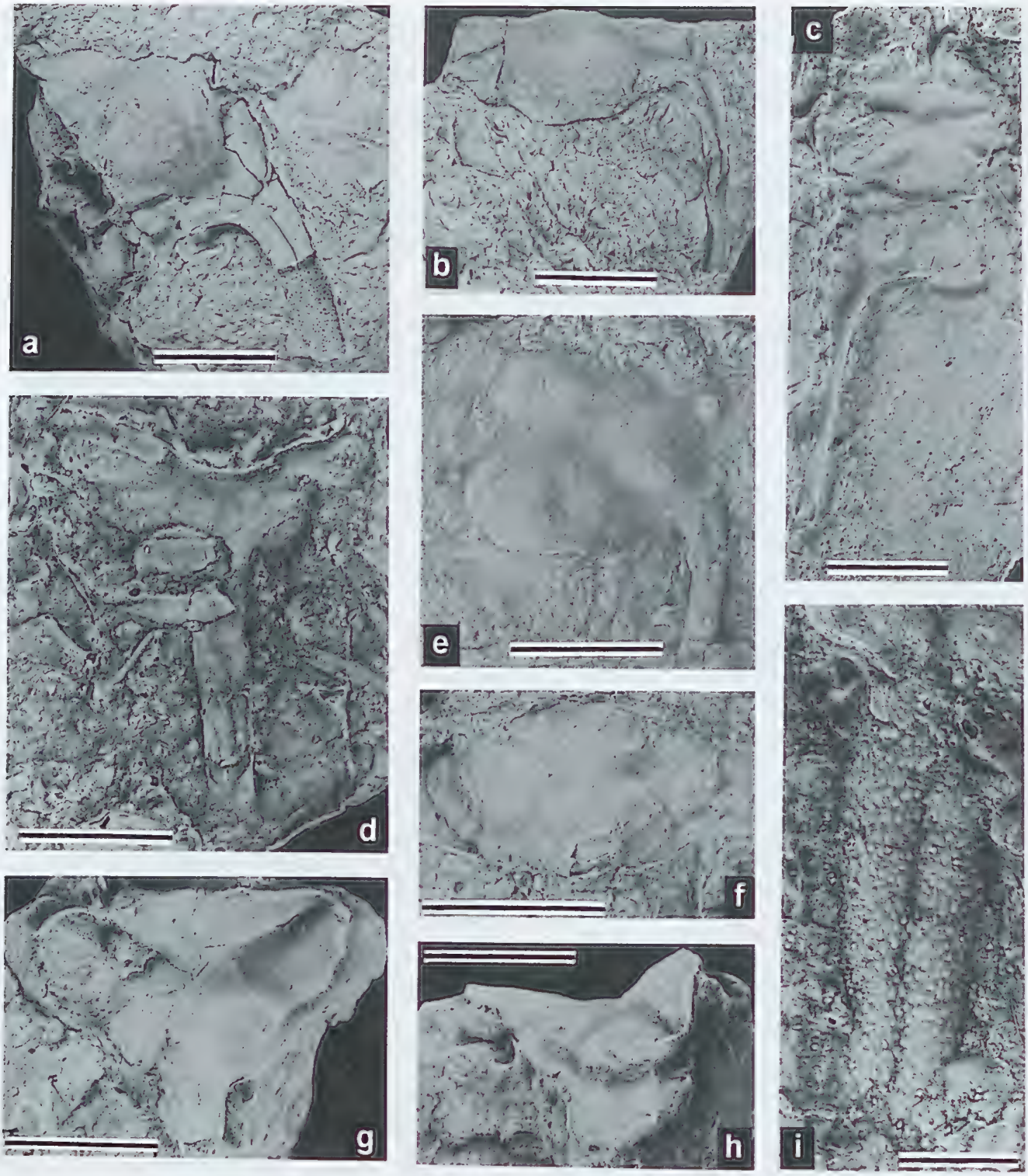

Figure 11. *Maldybulakia angusi* n.sp. Scale bars 10 mm except *i*, 5 mm. Latex casts from external moulds except *a, b, g, h*, internal moulds. (*a*) dorsal view of posteriormost B-pleurotergite AM F.102573. (*b*) dorsal view of posteriormost B-pleurotergite AM F.102574. (*c*) dorsal view of B-pleurotergite AM F.102575, with ventral view of another B-pleurotergite. (*d*) dorsal view of caudal pleurotergite AM F.102576. (*e*) dorsal view of posteriormost B-pleurotergite AM F.102577. (*f*) dorsal view of B-pleurotergite AM F.102578. (*g,h*) dorsal and right lateral views of caudal pleurotergite AM F.102579. (*i*) dorsal view of spine AM F.102580, probably paratergal spine of posteriormost B-pleurotergite.

ventral surfaces of spine bisected by shallow furrow along all but proximalmost part. Small and moderate sized tubercles abundant on lateral and median lobes of metazonite, somewhat stronger on lateral lobes.

B-pleurotergite of uncertain position (Fig. 10e,g) with short, posterolaterally directed paratergal spines. Prozonite relatively elongate, about 35 percent length of tergite. Short anterolaterally-directed, conical process at anterolateral corner of metazonite. Posteromedian spine on median lobe of metazonite varying from absent (Fig. 10g) to strong (Fig. 10e), variably more posteriorly- or dorsally-directed. Tubercles on lateral lobes of metazonite faint to moderately strong; tubercles weaker on median lobe, sometimes obscure.

B-pleurotergites (probably second or third) from middle of tagma (Fig. 10a,c,d) with prozonite about 25 percent length of tergite. Anterolateral corner of pleurotergite extended as a short angulation that gently rises distally. Robust tubercles usually present, abundant on lateral and median lobes of metazonite. Polygonal sculpture grading into transversely elongate, scaly sculpture along anterior margin of prozonite and posterior margin of metazonite and fine tubercles on paratergal spines. Lateral lobes relatively longer than on first B-pleurotergite, less inflated. Paratergal spine long, more posteriorly directed than that on first B-pleurotergite, nearly straight or gently curved for much of length, with slightly stronger posterior curvature distally; spine flattened proximally, more rounded near tip; rounded, ventrally directed process on posterior margin at base of paratergal spine.

Posteriormost B-pleurotergite (Fig. 11a,b,e) with prozonite up to 35 percent length of tergite. Anterolateral corner of metazonite forming a blunt, gently swollen angulation, separated from lateral lobe by shallow furrow. Median lobe relatively narrow, raised central part set off by pair of shallow longitudinal furrows. Tuberculation of median and lateral lobes subdued in most specimens. Paratergal spine long, approximately straight, weakly directed inwards, markedly flattened in section along entire length; longitudinal furrow on dorsal and ventral surfaces of spine deeper than on other pleurotergites, narrow but well-incised; spines with sculpture of small, crowded tubercles.

Caudal pleurotergite (Fig. 11d,?f,g,h) with teardrop shaped or subtriangular lateral lobes; lobes substantially inflated, tuberculate, set off from median lobe by furrows of similar depth to or shallower than those on other B-pleurotergites; outer edge of lateral lobes steep, set off from more gently sloping outer border by shallow furrow. Lateral margin strongly convex outward. Median spine gently upturned, of about even width along entire known length, bisected by shallow longitudinal furrow.

Telson sclerites unknown.

Discussion. Although *Maldybulakia angusi* is distinguished from its congenerics by numerous autapomorphies, a separate genus cannot be upheld unless reasonable synapomorphies are identified for *M. malcolmi* and *M. mirabilis*. As noted above, most of the similarities between the latter pair of species are probably symplesiomorphies

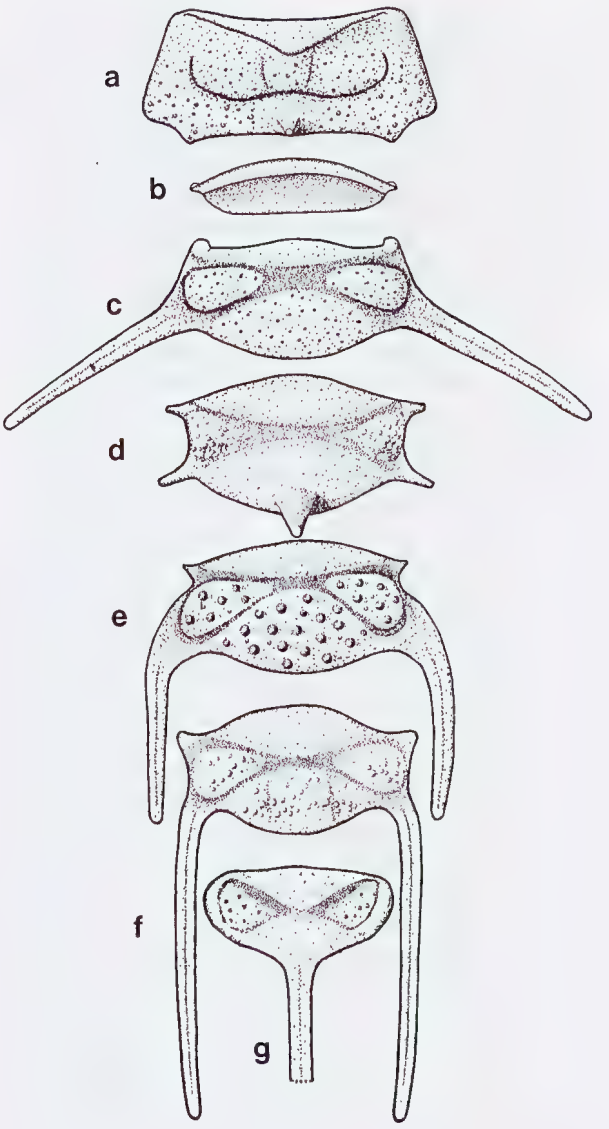

Figure 12. *Maldybulakia angusi* n.sp. Reconstructions of discrete morphological classes of trunk sclerites, indicating minimal number of tergites. (*a*) T-tergite. (*b*) ring tergite. (*c*) inferred anteriormost B-pleurotergite. Median spine on metazonite sometimes present. (*d*) B-pleurotergite of uncertain position. Presence of posteromedian spine is variable. (*e*) B-pleurotergite from middle part of tagma. (*f*) inferred posteriormost B-pleurotergite. (*g*) caudal pleurotergite.

and, if so, restricting *Maldybulakia* to these two species would recognise a paraphyletic group. In fact, certain characters might instead serve to unite the two Australian species to the exclusion of *M. mirabilis*. The flattened, sloping anterior scarp on the prozonite of the T-tergite is a distinctive modification shared by these two species but appears less developed in *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1g).

Considerable variability is observed in the strength of tuberculation on T-tergites as well as B-pleurotergites in *M. angusi*. Some specimens have only weak expression of tubercles (Figs. 9b, 10e, 11e), whereas most show them to

be more distinct or pronounced. Because of continuous gradation in tuberculation in otherwise similar tergites this is not regarded as an important criterion for distinguishing different pleurotergites. Presence or absence of a median spine on the metazonite is a feature that varies between tergites that are otherwise similar. This is observed on the T-tergites (compare Fig. 9b and 9g) as well as on various B-tergites that appear to represent the same position (e.g., Fig. 10b versus 10h; Fig. 10e versus 10g). Presence or absence of a median spine is considered to vary between individuals.

The antero-posterior position of B-pleurotergites can be largely determined based on the progressively more posterior direction of the paratergal spines on posterior segments (as observed analogously in other spiny myriapods, such as euphoberiid diplopods). Consistent with this line of evidence are other correspondences with known positions in *M. malcolmi*: the anterior pleurotergites are shorter relative to their width, and the anteriormost B-pleurotergite is distinguished by its anterolateral processes on the prozonite (Figs. 10f, 12c; compare with Fig. 6d). The posteriormost B-pleurotergite (immediately anterior to the caudal pleurotergite) is identified by its posteriorly-directed paratergal spines and relatively long median lobe on the metazonite (Figs. 11a,b,e, 12f).

Given the above considerations, the minimal number of sclerites in the trunk of *Maldybulakia angusi* is depicted in Fig. 12. The B-pleurotergites can be sorted into four morphological groups (Fig. 12c–f), excluding the caudal pleurotergite (Fig. 12g), thus allowing that the number of pleurotergites may be identical to that in *M. malcolmi* and, apparently, *M. mirabilis*. The position of the B-pleurotergite reconstructed in Fig. 12d is uncertain, constrained only by the likelihood that those shown in Figs. 12c and 12f are the first and last in the series based on their morphological correspondences to *M. malcolmi*. The specimen in Fig. 11f conforms to a caudal pleurotergite except for the absence of a median spine, although this is possibly due to breakage. Its lensoid outline (i.e., absence of paratergal spines) with tightly curved lateral margins is similar to caudal pleurotergites that have a median spine (Fig. 11g). In *M. malcolmi*, this specimen is most comparable to a lensoid specimen regarded as a caudal pleurotergite (Fig. 5c).

The best preserved external moulds display a cuticular sculpture of dense polygonal depressions amidst a maze of low ridges (Fig. 10i), as is also seen in *M. malcolmi* (Fig. 5j,k) and *M. mirabilis* (Tesakov & Alekseev, 1992: fig. 1i). This character is, accordingly, general for *Maldybulakia*.

Phylogenetic affinities

In the absence of information on cephalic structure, appendages, position of the gonopore, and genital morphology, the position of *Maldybulakia* within the Arthropoda is contentious. The discussion below outlines evidence in favour of myriapod affinities, and is followed by evidence that weakens the most likely alternative, a relationship to Crustacea.

Myriapoda. Tesakov & Alekseev (1992) recognised *Maldybulakia* as myriapod-like based upon the relative serial homonymy of the trunk tergites of *M. mirabilis* and the interpretation that the B-pleurotergites correspond to diplosomites. As noted above, I have accepted that the T-tergite and B-pleurotergites of *Maldybulakia* are similar in their construction to diplo(pleuro)tergites.

Evidence from serial variation in the trunk must now consider the fact that *Maldybulakia* possesses two well-differentiated trunk tagmata, as well as the fact that some species (such as *M. angusi*) display considerable serial variation within the two tagmata (this, however, very likely being specialised relative to the more homonymous condition of *M. malcolmi*). The extent of tagmosis in *Maldybulakia* exceeds that known for any myriapod, living or fossil. However, being a primitive attribute of atelocerates (or, for that matter, arthropods), a homonymous trunk is not a shared derived character of myriapods and does not provide positive evidence for group membership. The tagmosis of *Maldybulakia* could only be used to negate myriapod affinities if it can be shown to be shared with some other group of arthropods. There is little compelling evidence for drawing parallels between the two trunk tagmata of *Maldybulakia* and, for example, the thorax and abdomen of Hexapoda or pereion and pleon of Crustacea.

Myriapoda has been repeatedly dismissed as a paraphyletic grade group (Dohle, 1980, 1997; Kraus, 1997; Kraus & Kraus, 1994, 1996), although this interpretation conflicts with molecular studies that support myriapod monophyly (Regier & Shultz, 1997; Wheeler, 1998). Only two characters are repeatedly cited by Kraus (e.g., 1997) to unite the Progoneata with Hexapoda to the exclusion of Chilopoda and both of these are contentious. One, a maxillary plate with the ventral side of the mouth bordered by the second maxillae, is disputed by embryological, innervation, and muscular evidence that pauropods and diplopods lack second maxillae (Dohle, 1997, contra the claims of Kraus & Kraus, 1994, 1996 based on external morphology). The second, coxal vesicles and styli, exhibits considerable homoplasy (e.g., absences of both in many diplopods; absence of styli in pauropods and Ellipura) and homologies are dubious. Notably, eversible vesicles in some groups (e.g., the pair of sacs at the end of the *Ventraltubus* in Ellipura) are of appendicular nature, whereas those of others are extra-appendicular (Matsuda, 1976). The latter include the vesicles of Symphyla, which arise on the so-called "ventral organs" associated with gangliar formation (Tiegs, 1940), these being segmental thickenings of the embryonic ventral ectoderm. The paraphyly hypothesis denies that any synapomorphies can be identified to defend membership in "Myriapoda"—the defining characters of the group are more general, basal for Atelocerata. Incomplete preservation does not permit most of the putative atelocerate apomorphies to be checked in *Maldybulakia*: such features include uniramous limbs, Malpighian tubules, suppression of the second cephalic somite, a cephalic fat body, loss of the mandibular palp, molar hooks on the mandible, Tömösváry organs, a single pretarsal (depressor) muscle, and anterior tentorial arms. Characters that have alternatively been used to define a

monophyletic Myriapoda, such as the "swinging" tentorium (Manton, 1964), a mandibular gnathal lobe, and loss of the median eyes, will rarely be known from fossils, and likewise cannot be checked in *Maldybulakia*.

In spite of the preponderance of missing data, the presence of tracheae is inferred based on the interpretation of openings in the pleural furrow in *M. malcolmi* as spiracles. Tracheae have traditionally been regarded as a synapomorphy for atelocerates, although some workers have cautioned that the variable position of spiracles may imply multiple origins of a tracheal system (Kraus & Kraus, 1996; Kristensen, 1991). The hypothesis of multiple origins of tracheae has been taken to an extreme by Dohle (1997) and Kraus (1997), both of whom regard a tracheal system evolving independently at least four to six times in Atelocerata. The interpretation of the lateral exoskeletal component as pleural also implies atelocerate affinities for *Maldybulakia*. Manton (1979) recognised that myriapods and hexapods shared pleural structures not shared with other arthropods, including the development of pleurites.

At a less general level, a trunk composed of diplotergites suggests affinities to various subgroups of myriapods, notably Diplopoda, Arthropleuridea, and Kampecarida. Although representing three classes (Shear, 1997), available evidence suggests these taxa are closely related, the latter two extinct classes apparently allied to the Dignatha. Comparison with *Kampecaris* Page, 1856 (Přídolí-early Pragian, Great Britain) reveals some similarities that may suggest a relationship. A detailed exposition on the morphology, affinities, and habits of *Kampecaris* was undertaken in an unpublished thesis by Almond (1986), partly summarised by Shear (1997). *Maldybulakia* and Kampecarida share a few distinctive characters that are also shared by millipedes. These include a heavily-calcified tergal exoskeleton and a posterior trunk with posteriorly-overlapping diplotergites (diplosegmentation in *Kampecaris* is confirmed, the legs being known). The sternum of *Kampecaris* was described by Almond as poorly known, in contrast to a strongly calcified tergum with ball-and-socket intertergal articulations, which is similar to the case in *Maldybulakia* (for which the lack of sternites—compared to hundreds of tergites—is strong evidence for their lack of mineralisation). *Kampecaris* shares a few other characters with millipedes that cannot at present be checked in *Maldybulakia* (e.g., limbs articulating wholly with the sternites; a long femur and simple, pointed tarsus). Almond (1986) excluded *Kampecaris* from the Diplopoda, suggesting a high-level taxonomic separation. His basis for this was several novel features of *Kampecaris* that are not shared by any diplopod. These include a subdivision of the head by a transverse suture or articulation into two subunits, an inflated caudal tagma, and the tergal cuticle perforated by sizable, closely spaced canals. *Maldybulakia malcolmi* likewise displays large, densely arranged pores on the cuticular surface (Fig. 8b) that run through the cuticle as vertical canals (Fig. 8a), while Tesakov & Alekseev (1992: 22) described similar pores in *M. mirabilis*. It is possible that the pore/canal structure of the cuticle in *Maldybulakia* and Kampecarida is a shared, derived character of these two groups of mid-Palaeozoic taxa. It is doubtful that these large canals are the homologues of the gland ducts in extant myriapod cuticles (Blower, 1951), which are much finer structures.

Maldybulakia is readily distinguished from *Kampecaris* by its uniquely derived characters (notably differentiation of trapezoidal and bilobate pleurotergites) and the lack of certain autapomorphies of *Kampecaris* (e.g., the inflated caudal tagma). These do, not, however, negate the possibility of a close relationship between them. Almond (1985) interpreted the tail plate of *Kampecaris* as a modified diplotergite, an interpretation that also applies to the caudal pleurotergite of *Maldybulakia*.

There is little evidence at hand to ally *Maldybulakia* closer to diplopods than to *Kampecaris*. The association of pleural elements with the metazonites in varying degrees of coalescence to form pleurotergites was noted by Hoffman (1969: 586) as characteristic of nearly all helminthomorph diplopods, and regarded by Enghoff (1984) as a synapomorphy of eugnathan diplopods that evolved independently in platydesmids. Homology of the metazonal pleurotergites in millipedes and *Maldybulakia* must be regarded with suspicion given the relatively derived position of the Eugnatha within the Diplopoda. The condition of pleurites in Kampecarida is uncertain. Almond (1986) noted the absence of free pleurites but allowed that they could be fused to the tergum to form pleurotergites. Similarities to large, spiny millipedes, notably Carboniferous euphoberiids, are very likely superficial. Euphoberiids such as *Myriacantherpestes* Burke, 1979, do not have trunk tagmosis (versus the marked separation of the trapezoidal and bilobate tergites in *Maldybulakia*). The long-spined bilobate pleurotergites of *Maldybulakia angusi* display a superficial resemblance to *Myriacantherpestes* that is less strong in the other species of *Maldybulakia*. Details of tergite construction, however, fail to support an especially close relationship. Likewise, it is not possible to identify any features shared by *Maldybulakia* and Arthropleuridea that are not also shared with Kampecarida and Diplopoda. The simple overlap of the tergites in arthropleurids differs strikingly from overlap on the prozonite of *Maldybulakia* and, as noted above for diplopods, arthropleurids do not display trunk tagmosis.

Crustacea. The plasticity of exoskeletal morphology observed within the malacostracan crustaceans, notably in such groups as Isopoda, suggests the possibility that *Maldybulakia* could be accommodated within the Malacostraca. It is considered unlikely that *Maldybulakia* could belong to any malacostracan (or indeed crustacean) group with a carapace, as all sites preserving *Maldybulakia* lack any carapace remains (the same argument would apply to chelicerate assignments, based on the absence of a prosoma). Given the apparently different taphonomic histories at each of the three sites it seems exceedingly improbable that all three would preserve abdominal (or opisthosomal) tergites in abundance without a single carapace (or prosoma). Evidence has already been given for why the T-tergite is regarded as a trunk tergite rather than as a cephalic shield.

The small number of tergites in *Maldybulakia* conflicts with the post-cephalic segmentation of malacostracans, which have eight thoracic somites (pereonites) and seven abdominal somites (pleonites). Specimens such as the holotype of *M. malcolmi* are regarded as posteriorly complete (the caudal pleurotergite and telson sclerites comprising a typical arthropod body termination). As such, a malacostracan model that accounts for the observed shortfall of segments by positing unpreserved pleonites is unacceptable. In order to accommodate the post-cephalic segmentation of malacostracans in *Maldybulakia* it is necessary to make such conjectures as the caudal pleurotergite incorporating the entire pleon (which is possible, by comparison to the pleotelsons of some isopods, although atypical), in which case the putative pereon is still too short, even if the ring-like tergite is considered a separate pereonite.

A malacostracan crustacean hypothesis might interpret the lateral opening in the third B-pleurotergite as a gonopore. Although accounting for the singularity of this structure, it is weakened by the fact that malacostracan gonopores are typically associated with the coxae or the sternite medial to the coxae, rather than the pleuron. It also requires that this segment be the sixth (female) or eighth (male) pereonite, which puts severe constraints on the more posterior tergites (demanding that they incorporate the entire pleon if not also part of the pereon). In summary, a myriapod interpretation incorporates more positive character evidence and conflicts with less evidence than a crustacean interpretation.

Euthycarcinoidea. A reviewer of this paper encouraged a comparison between *Maldybulakia* and the Euthycarcinoidea. Euthycarcinoids, known from ten aquatic species of Silurian to Triassic age, have been assigned to nearly every major group within the Arthropoda (see Schram & Rolfe [1982] for an overview of euthycarcinoid morphology). The most recent assessment of myriapod fossils (Shear, 1997) concluded that atelocerate affinities for euthycarcinoids can neither be ruled out nor strongly supported. A close relationship between euthycarcinoids and *Maldybulakia* is dubious given that trunk tagmosis in the former group involves a wide preabdomen and a narrow postabdomen. *Maldybulakia* clearly lacks this style of tagmosis. Furthermore, most euthycarcinoids have serially variable lengths of the preabdominal tergites, these corresponding to varying numbers of sternites and appendages, and homologues of the pleurites of *Maldybulakia* are absent. A comparison could, however, be made between the specialisations of the anterior tergites of the trunk in the two groups. Euthycarcinoids have an enlarged first preabdominal tergite followed by a reduced haplotergite, with the apparently corresponding positions in *Maldybulakia* being the T-tergite and ring tergite. At present, no other potentially synapomorphic characters are identified to support a particularly close relationship between *Maldybulakia* and Euthycarcinoidea.

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The Upper Devonian Fish *Bothriolepis* (Placodermi: Antiarchi) from near Canowindra, New South Wales, Australia

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ABSTRACT. The Upper Devonian fish fauna from near Canowindra, New South Wales, occurs on a single bedding plane, and represents the remains of one Devonian palaeocommunity. Over 3000 fish have been collected, predominantly the antiarchs *Remigolepis walkeri* Johanson, 1997a, and *Bothriolepis yeungae* n.sp. The nature of the preservation of the Canowindra fauna suggests these fish became isolated in an ephemeral pool of water that subsequently dried within a relatively short space of time. This event occurred in a non-reproductive period, which, along with predation in the temporary pool, accounts for the lower number of juvenile antiarchs preserved in the fauna. Thus, a mass mortality population profile can have fewer juveniles than might be expected. The hypothesis that a single species of *Bothriolepis* is present in the Canowindra fauna is based on the consistent presence of a trifid preorbital recess on the internal headshield and separation of a reduced anterior process of the submarginal plate from the posterior process by a wide, open notch. Principal Components Analysis (PCA) based on head and trunkshield plate measurement shows no separation of *Bothriolepis* individuals into distinct clusters and is consistent with this hypothesis. A wide range of plate shape variation can thus occur within a species of *Bothriolepis*, and caution should be used when separating species on this basis in the future.

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In 1993, Alex Ritchie (Australian Museum) collected approximately 3000 fish from a single layer within the Upper Devonian Mandagery Sandstone, at a site approximately 10 km southwest of Canowindra, along the road to Gooloogong (Fig. 1). The recovery of these fish from a single bedding plane suggests these fish lived and died together, representing the remains of a palaeocommunity. Thus, the Canowindra fauna provides an opportunity to describe the nature and structure of an Upper Devonian fish community, although it must be remembered that the total community has not been preserved. The crowding of fish on the layer suggests a mass mortality during dry conditions. Additionally, the large number of well-preserved specimens of *Bothriolepis* present allows for a determination of the range of variation in head and trunkshield plate proportions that could be expected within a single species.

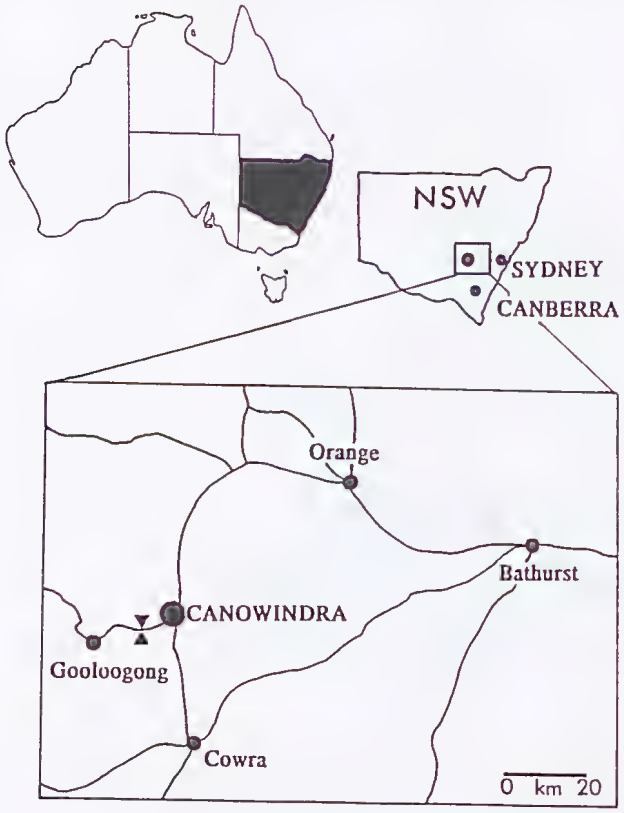

Figure 1. Map showing locality of Canowindra fauna, Mandagery Sandstone. From Johanson & Ahlberg, 1997.

The fauna is dominated by the antiarchs *Bothriolepis yeungae* n.sp. and *Remigolepis walkeri* Johanson, 1997a, and less commonly, the euarthrodire *Groenlandaspis* Heintz, 1932. Sarcopterygians are rare, including the canowindrid *Canowindra grossi* Thomson, 1973, the tristichopterids *Mandageria fairfaxi* Johanson & Ahlberg, 1997, and *Cabonnichthys loomesi* Ahlberg & Johanson, 1997, the rhizodontid *Gooloogongia loomesi* Johanson & Ahlberg, 1998, and two specimens of the dipnoan *Soederberghia* Lehman, 1959. No other vertebrates (e.g., tetrapods), plants or invertebrates have thus far been observed.

In 1993, nearly 195 rock slabs of varying sizes were collected from the Canowindra locality, but attempts to record the sequence of rocks as they were removed from the layer were largely unsuccessful. The counterpart of the collected fish layer remains *in situ*, preserving the original positions of these rock slabs and the fish on them. Due to time limitations, sedimentological features of the rocks above and below the fish layer were not recorded. This layer was completely covered to prevent vandalism, and is not currently available for examination (but will be uncovered in the future).

Nevertheless, information regarding various aspects of the preservation of the fish can be obtained from separate slabs and extrapolated to the fauna as a whole. Information as to the demise of the fauna can be garnered by considering the taphonomic aspects of the fauna, including events or processes occurring both before and after death (Behrensmeyer & Kidwell, 1985; Wilson, 1984, 1996). Population profiles of the antiarchs can indicate the relative abundances of juveniles and adults in the community, and can be compared to profiles expected when death is either catastrophic or attritional (e.g., Wilson, 1988). Differences in population profiles are also of interest, and can be used to speculate on timing of reproduction, growth rates, and prevalence of predation.

More than 1300 individuals of *Bothriolepis* from Canowindra have been noted to date, and, when preserved, a trifid preorbital recess and a reduced anterior process of the submarginal are consistently present. The first character is present in several species of *Bothriolepis*, while the second character appears to be unique to this species. In combination, they suggest that one species of *Bothriolepis* is present at Canowindra. This hypothesis is tested by performing a Principal Components Analysis (PCA) on head and trunkshield measurements on the individuals in this fauna.

Materials and methods

The Canowindra fauna is preserved as three-dimensional natural moulds filled with hardened sandstone casts, preserving the external and internal surfaces of the dorsal head and trunkshield plates, respectively. Latex casts were taken of both surfaces, whitened with ammonium chloride, and photographed. Labelled line drawings were made from these photographs or using a camera lucida. Measurements used in the PCA were taken from the maximum length and width of plates in the midline of the head and trunkshield (see Abbreviations, below) and from the orbital fenestra. Ratios given in the descriptive section are taken from the average of these measurements.

Specimens in the Canowindra fauna have been flattened and distorted to a certain degree. The degree of distortion was determined with the assistance of Dr D. Durney, School of Earth Sciences, Macquarie University. Latexes of the larger rock slabs (preserving a large number of individuals) were photographed, and the head and trunkshield outlines of *Bothriolepis* were drawn on overlying tracing paper. An image of these outlines and their relative orientations were taken and entered into a computer application developed by D. Durney. Using this, the distortion of these outlines from the ellipse was determined, and the amount and direction of shear affecting the specimens on the slab calculated. The amount of distortion was equivalent on the 8 slabs tested and was minimal (approximately 2–5%, as indicated by the appearance of the specimens themselves). The general direction of shear can be determined on each slab, but relating these to one another and to direction of cleavage in the rock will have to wait until the Canowindra site is reexcavated and the position of these slabs determined.

If a specimen lies exactly along the axes of the direction of cleavage, distortion can make them narrow and long (Fig. 3B) or short and broad (Fig. 3D), with no apparent

angular distortion (G.C. Young, pers. comm.). This could result in misleading impression of the degree of distortion in the fauna, but this would only occur in those specimens lying exactly along the axes of distortion. These would surely be very low in number relative to all other specimens not lying exactly along these axes (e.g., Fig. 4C). Because of this, and because overall distortion does not appear to be substantial, measurements can be confidently taken and used in a PCA without further correction.

Australian Museum specimen registration numbers are prefixed "AM F". Figures in the present work are referred to using the abbreviation Fig. or Figs., reference to other figures is indicated by use of lower case—fig. or figs.

Principal Components Analysis

Seventy-seven better preserved specimens of *Bothriolepis* were identified in the Canowindra fauna and measurements taken from midline plates as described above. Lateral plates were often crushed post mortem so that measurements could not be confidently and consistently made. Measurements were taken with a vernier caliper to the nearest 0.05 or 0.1 mm, and subjected to a PCA to test the initial hypothesis (Ho) that a single species of *Bothriolepis* is present at Canowindra. Clusters of individuals can be recognised visually through ordination of the results of the PCA, where the position of individuals is plotted using the components as the X and Y axes (Abbott *et al.*, 1985).

The effects of individual size must be removed from the data set before the PCA, because variation in shape is of taxonomic interest (e.g., Ciochon, 1993: 60). The majority of *Bothriolepis* individuals measured in this analysis were relatively large, with a range in head + trunkshield length from 76.6 to 190 mm, and a mean of 123.1 mm. Larger specimens were chosen for measurement as these were the best preserved and easiest to prepare for casting and study. Smaller specimens were very difficult to prepare (e.g., Fig. 6E,F), so that plate measurements could not be confidently taken.

Various methods for size removal have been suggested, with little agreement on the best method. A summary of these methods was provided by Reist (1985). Several address allometry, or unequal changes in shape during ontogeny. The morphology of juvenile *Bothriolepis* differs in many respects from adults (Stensiö, 1948; Werdelin & Long, 1986), and these differences would affect the results of this analysis, which is concerned with taxonomic rather than ontogenetic variation. However, because larger specimens of *Bothriolepis* were measured, allometric effects may not be substantial. To test this, measurements taken for *Bothriolepis* from Canowindra were regressed against the total head+trunkshield length in a simple linear regression (Sokal & Rohlf, 1981; Zar, 1996), where a slope other than one indicates allometry (e.g., Werdelin & Long, 1986). It is important to note that the regression method used is a Model I regression, requiring that the independent variable be error-free (Sokal & Rohlf, 1981). A Model II regression does not have this requirement, but can be controversial (e.g., Sokal & Rohlf, 1981: 550). Because the measurement of head and trunkshield length (independent variable X) was simple to consistently and confidently take from specimen to specimen, it is assumed to be error-free, and a Model I regression is used below.

The statistical program "Datadesk" was used in this and all subsequent analyses. All variables were log transformed to standardise variances. The null hypothesis was Ho: regression slope equals 1 (isometric change). The results of the regression (Appendix) indicated that the null hypothesis could only be accepted for four variables. In all others, allometry was indicated.

Thus, the choice of method to remove the effects of size before PCA must account for this allometry. One method not highly criticised by Reist (1985) is regression, such that the shape variate is represented by the deviation of each observed data point from the regression line describing the size relationship of the two variables. A predicted value is read from the regression line such that the observed point minus the predicted gives the shape variate (Reist, 1985).

Results of the Principal Components Analysis

The use of simple line regression to remove size appears to have had the desired results. To test the efficacy of size removal, Reist (1985) suggested regressing the transformed data against X: if the slope of the regression line is 0, then no relationship is present between the variables. Thus, the shape variate (Y) is independent of size (X), and size has been removed from the original variables. In this analysis, regressing transformed variables against size resulted in slopes of 0 for all variables. These shape variables were used in the PCA below.

The results of the PCA are shown graphically in Fig. 2A–C, with the first three Principal Components as the axes. A wide range of variation is shown by the distributions of various specimens on the graphs, and although certain specimens lie on the outer margins of this distribution, no grouping of individuals into distinct clusters is apparent. This suggests that variation in head and trunkshield plate shape is not sufficient to separate *Bothriolepis* from Canowindra into more than one species. This is consistent with the original hypothesis, that a single species of *Bothriolepis* is present in the fauna, and more importantly indicates that a certain range of variation in quantitative measurements can be expected within populations.

A similar result was obtained by Trinajstic (1995) for arthrodires from the Gogo Formation (Frasnian, Western Australia). Statistical analyses indicated that individuals assigned to two separate genera were in fact part of a continuous variation and thus should be part of the same species. These results demonstrate the care that should be taken when attempting to discriminate species on the basis of plate proportions. Besides the usual problems (distortion, breakage, etc.), consideration of only a small sample of individuals may indicate differences that would disappear as more individuals are sampled. Therefore, species diagnoses should stress qualitative characters. Quantitative characters may be included in the description, but the potential problems inherent in these characters should be recognised.

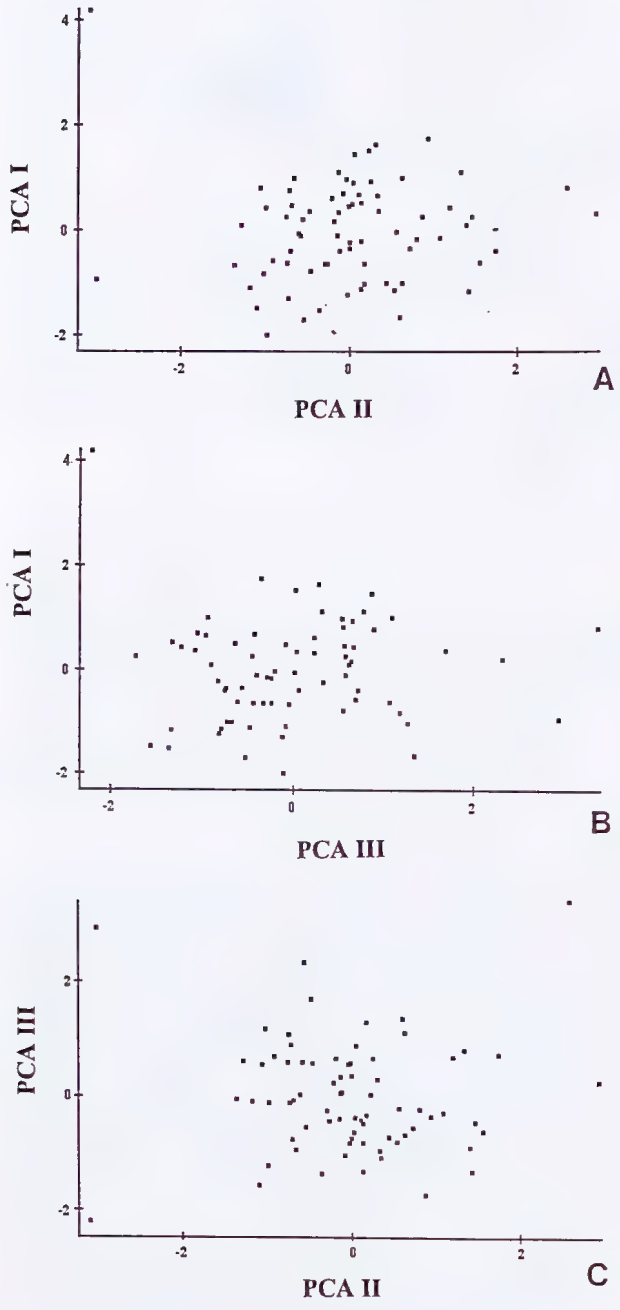

Figure 2. A, scattergrams of PCA axes I versus II. B, scattergram of PCA axes I versus III. C, scattergram of PCA axes III versus II. Dots indicate position of each of 77 specimens of *Bothriolepis yeungae* relative to these axes. Note that there is no separation of these individuals into different clusters, indicating that variation in plate measurements is not sufficient to differentiate more than one species of *Bothriolepis* at Canowindra.

Systematic palaeontology

Subclass Placodermi McCoy, 1848
Order Antiarchi Cope, 1885
Suborder Bothriolepidoidei Miles, 1968
Family Bothriolepidae Cope, 1886
Genus *Bothriolepis* Eichwald, 1840

Bothriolepis yeungae n.sp.

Figs. 3–10, 11C,J, 13–18

Bothriolepis sp. Conolly, 1965: 56.
Bothriolepis sp. Gilbert-Tomlinson, 1965: 208.
Bothriolepis sp. Long, 1982: 66.
Bothriolepis sp. Young, 1993: 251.
Bothriolepis sp. Johanson & Ahlberg, 1997: 39.
Bothriolepis sp. Ahlberg & Johanson, 1997: 653.
Bothriolepis sp. Johanson, 1997a: 213.
Bothriolepis sp. Johanson, 1997b: 201.

Holotype. AM F.101247, external head and trunkshield, left pectoral fin in dorsal view (Figs. 3A, 10G).

Other material. AM F.99692, AM F.100838–844, AM F.100885–904, AM F.101232–273, 101275–277, AM F.101608, AM F.101609, AM F.102397–399, AM F.105479–540, representing internal and external views of the head and trunkshield as well as disarticulated plates. Proportions given below are taken from specimens used in PCA, including (AM F.101247 and 105479–540). Measurements available from the author upon request.

Locality and horizon. 10 km SW of Canowindra, NSW, Australia, along the road to Gooloogong (33°35'56"S 148°33'59" E). The fossil fish layer is located within the Mandagery Sandstone (Upper Devonian).

Etymology. The species is named after Monica Yeung, Gondwana Dreaming Pty Ltd, Canberra, for her invaluable contributions to the Canowindra project.

Diagnosis. Differs from all other *Bothriolepis* in possessing a reduced anterior process of the submarginal, separated from the posterior process of the submarginal by a wide, open notch. Characterised by: Preorbital recess trifid. Oval attachment area for prelateral on the lateral plate small, laterally oriented, separated from a strongly developed, horizontal anterior submarginal attachment on the lateral plate. Posterior submarginal attachment on lateral plate ending at posterior margin of spiracular groove. Pineal plate with reduced posterolateral corners. Postlevator cristae of anterior median dorsal plate sharply defined and short, often dissociated from the postlevator thickenings and situated in the levator fossa. *Crista transversalis interna anterior* on anterior ventrolateral plate obliquely oriented. Cv2 and Mm1 plates do not overlap on mesial margin of pectoral fin.

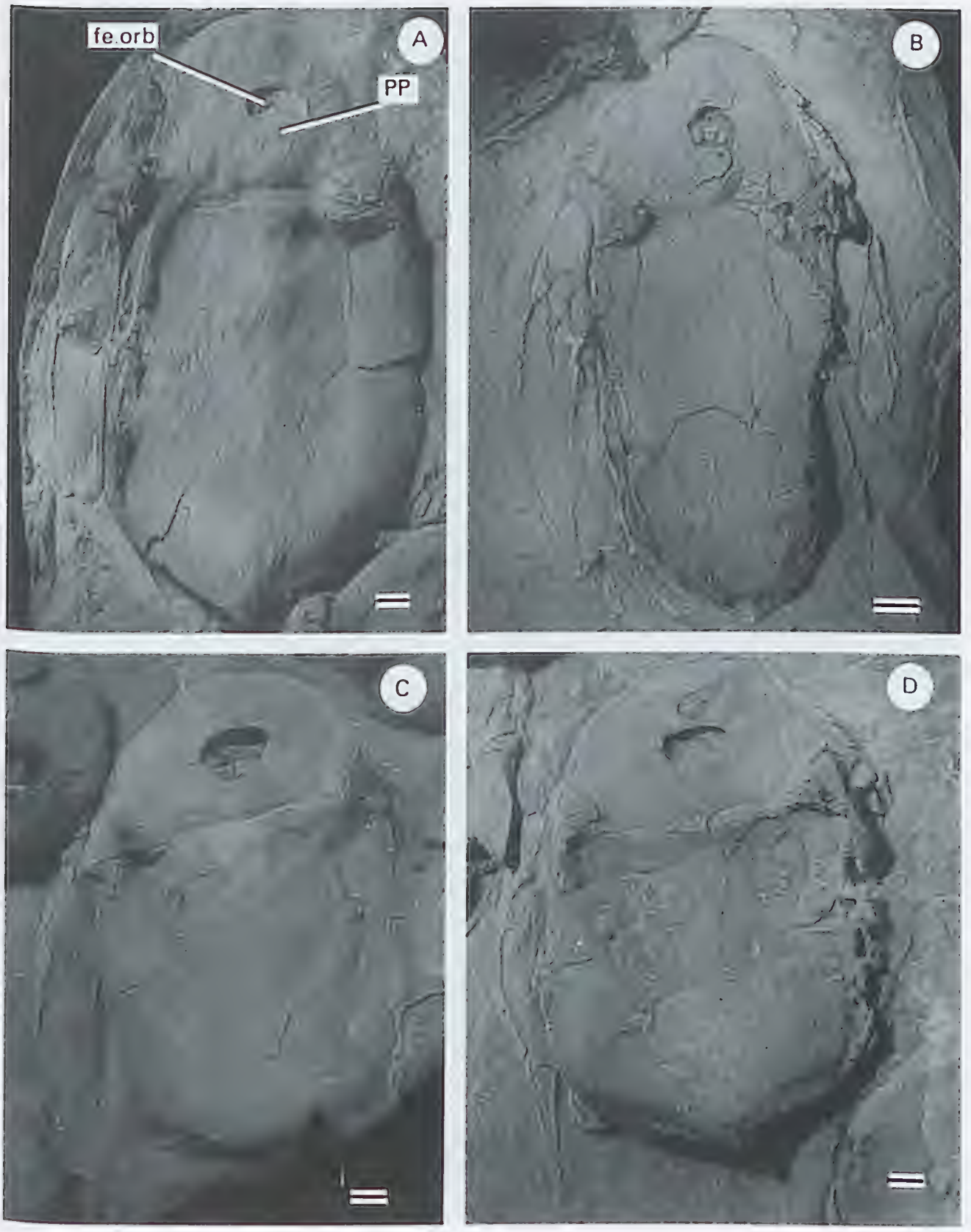

Figure 3. *Bothriolepis yeungae* n.sp. A, AM F.101247, holotype; B, AM F.100901; C, AM F.101271; D, AM F.101272; all dorsal view of head and trunkshield. Scale = 1 cm.

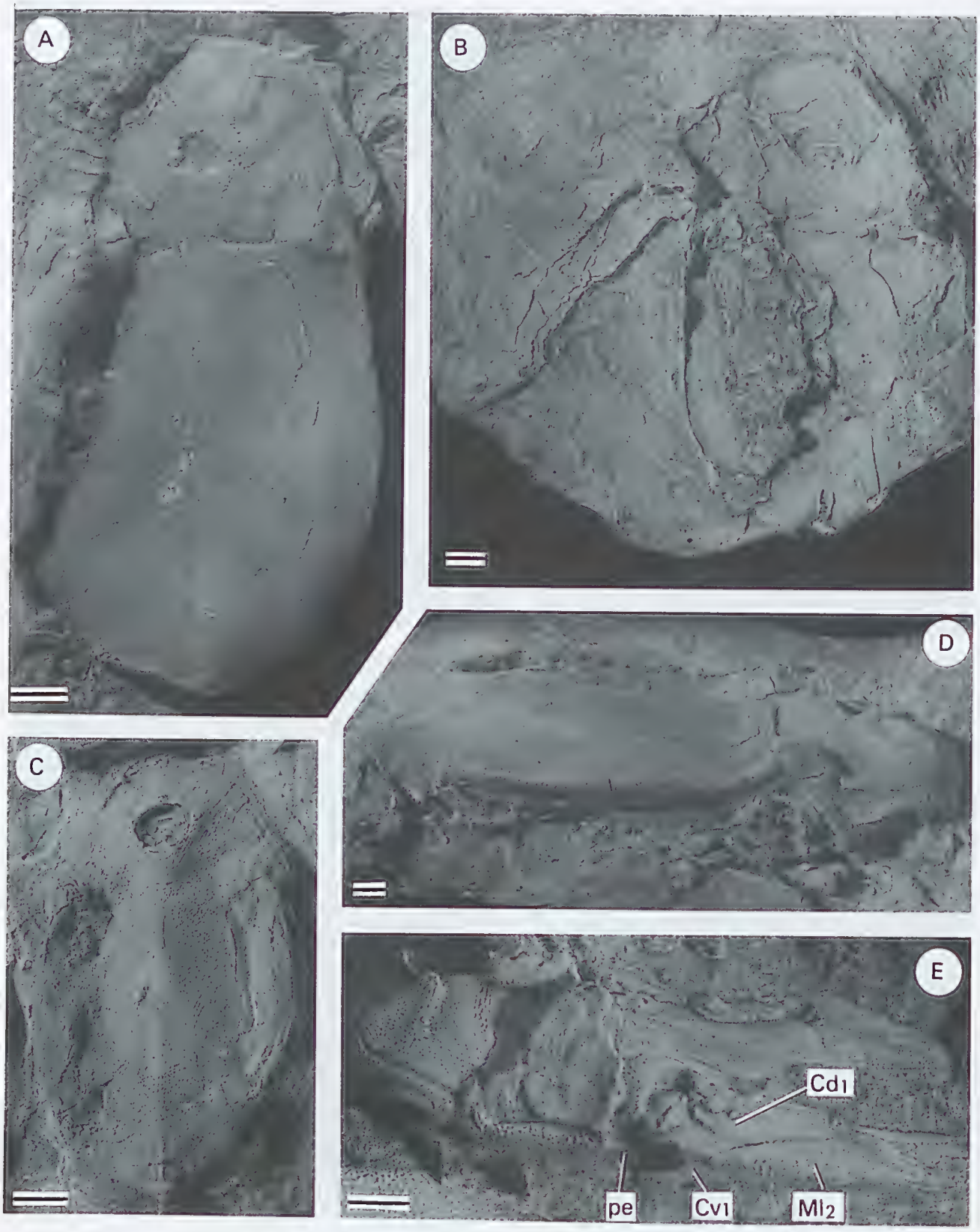

Figure 4. *Bothriolepis yeungae* n.sp. A, AM F.100891, dorsal view of head and trunkshield; B, AM F.100901, ventral or internal view of head and trunkshield; C, AM F.101241, dorsal view of head and trunkshield; D, AM F.100891, lateral view of head and trunkshield and partial pectoral fin; E, AM F.101250, lateral view of head and trunkshield with proximal plates of pectoral fin. Scale = 1 cm.

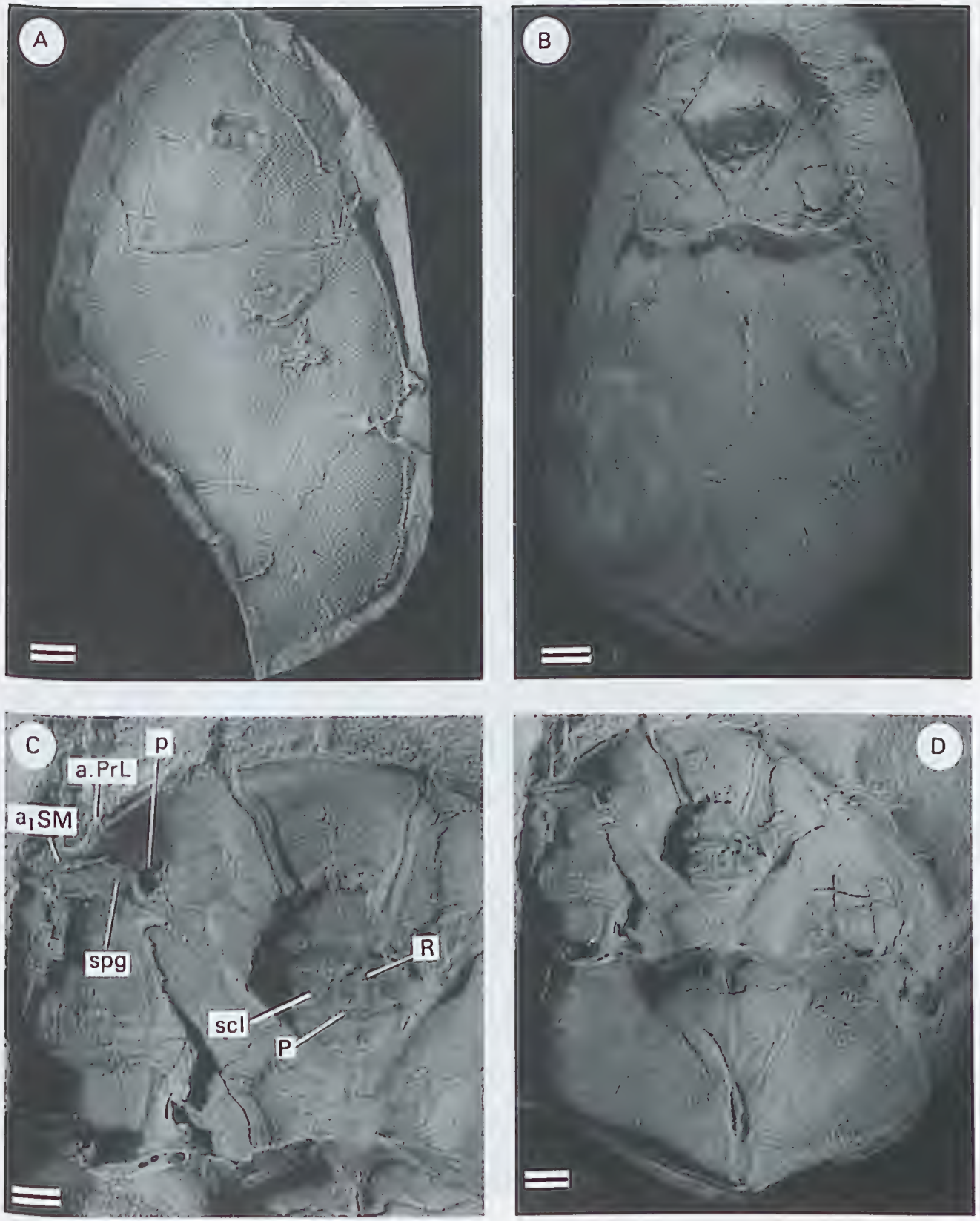

Figure 5. *Bothriolepis yeungae* n.sp. A, AM F.100802a, dorsal view of head and trunkshield; B, AM F.100802b, ventral or internal view of head and trunkshield, counterpart of Fig. 5A; C, AM F.100843, closeup of internal view of headshield; D, AM F.100843, internal view of headshield and anterior portion of AMD. Scale = 1 cm.

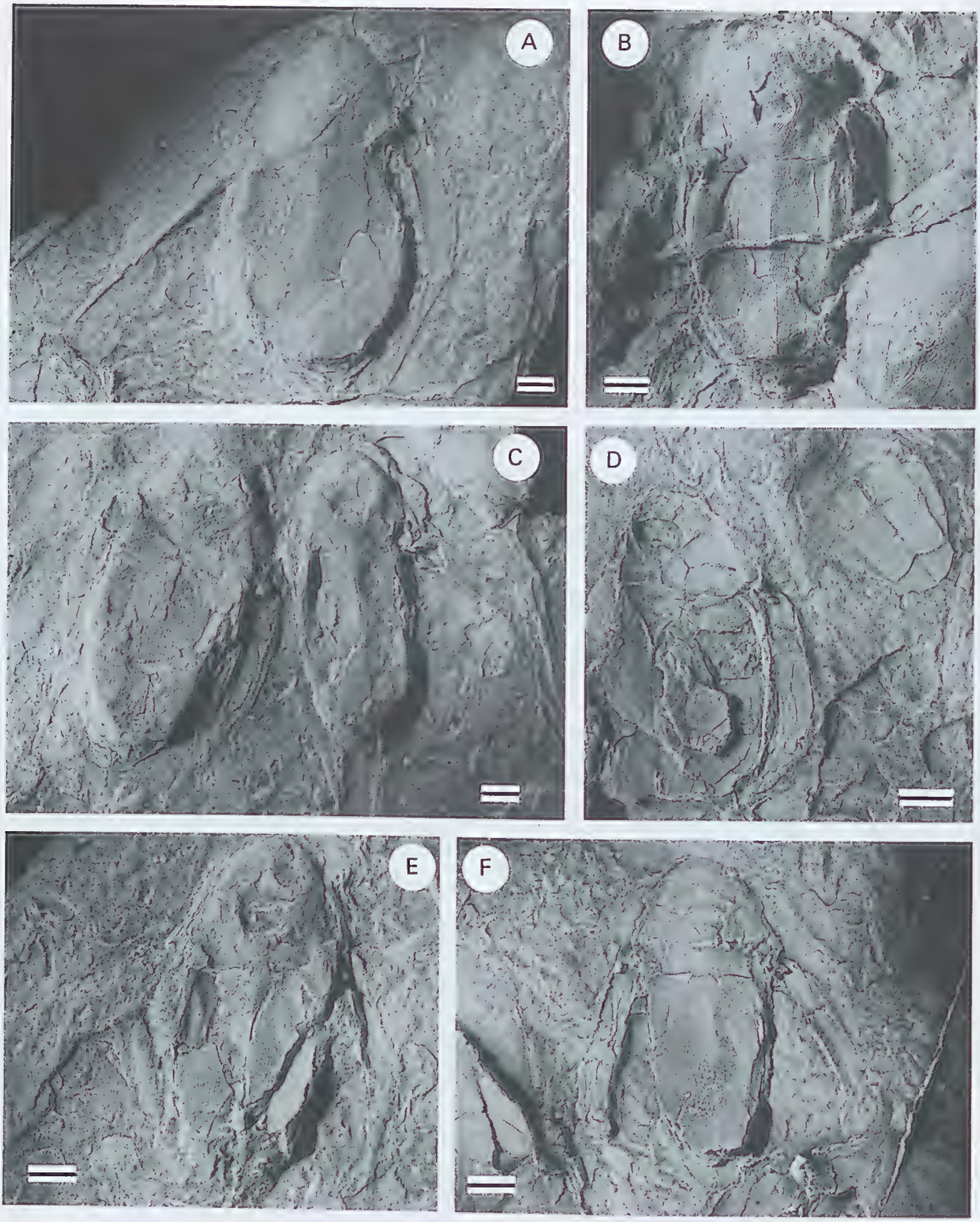

Figure 6. *Bothriolepis yeungae* n.sp., smaller individuals. A, AM F.101608; B, AM F.101243; C, AM F.101276, AM F.101277, all dorsal view of head and trunkshield; D, AM F.101274, AM F.101275 (PMD), internal view; E, AM F.102397; F, AM F.101240, both dorsal view of head and trunkshield, including pectoral fins (also Fig. 6A). Scale = 1 cm.

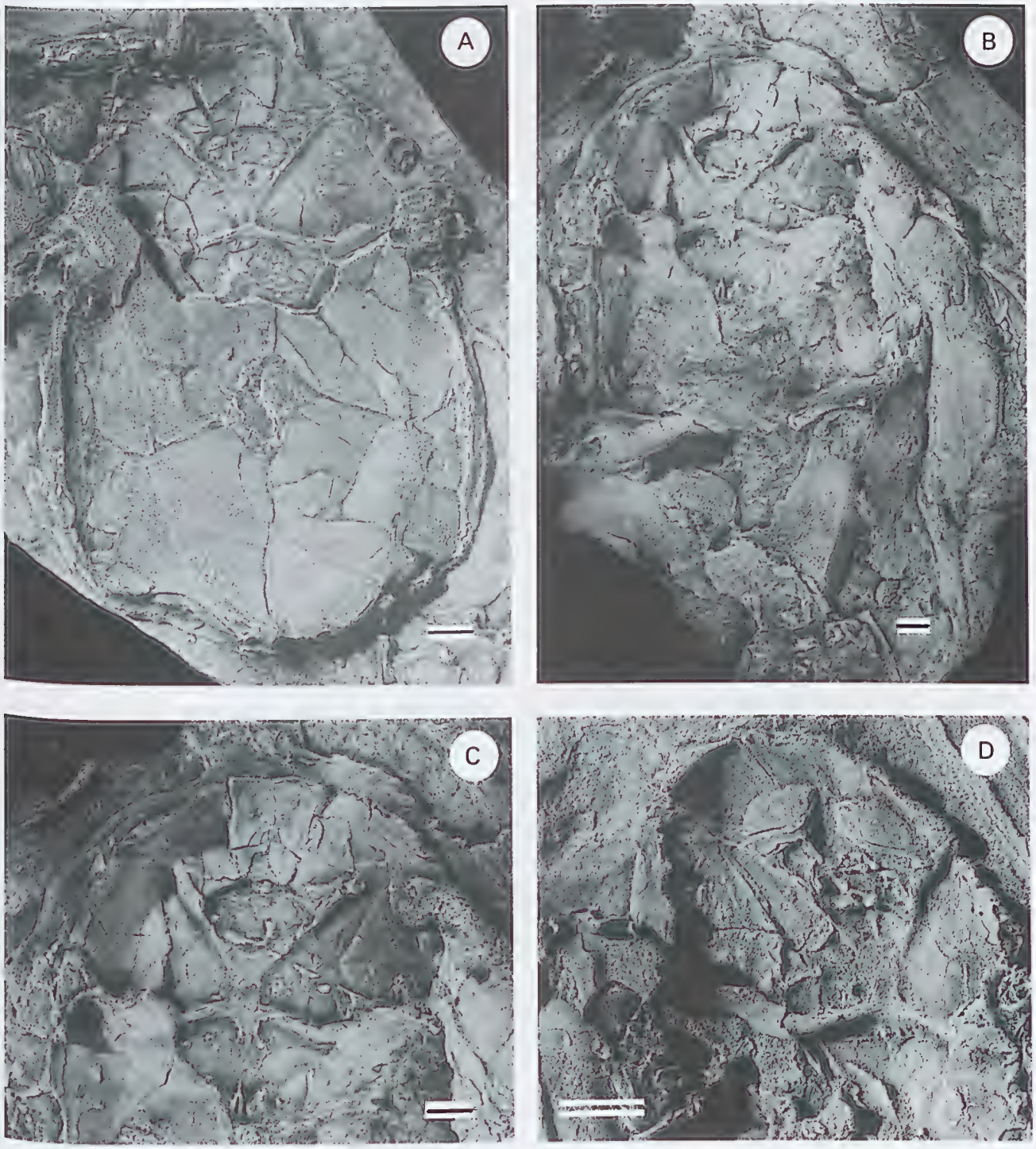

Figure 7. *Bothriolepis yeungae* n.sp. A, AM F.100893, ventral view of external trunkshield and internal view of headshield; B, AM F.101234, internal view of headshield, partial internal view of trunkshield; C, AM F.101234, closeup of internal view of headshield; D, AM F.100842, internal view of headshield with external view of suborbitals. Scale = 1 cm.

Remarks. Despite criticisms of quantitative measurements above, the diagnosis illustrates the difficulty in finding a large number of unique qualitative characters to diagnose species of *Bothriolepis*. However, the unusually low anterior process of the submarginal and the wide notch between this and the posterior submarginal process are present on all individuals of *Bothriolepis* from the Canowindra type locality.

A large number of specimens of *Bothriolepis* are available for examination, and the majority are well preserved (although flattened) with articulated plates in the head and trunkshield. The majority of specimens are

preserved in life position. Although this appears to be an ideal situation for species description and comparison, it is in fact limiting. Views of the internal surface of the head and trunkshield are present, but less common. The pectoral fin is most frequently preserved attached to the trunkshield so that the articular area on the anterior ventrolateral plate is not generally visible. Flattening of specimens means the medial wall of the pectoral fin is rarely visible, as are the plates comprising the lateral lamina of the trunkshield. These problems were also apparent in description of *Remigolepis walkeri* from Canowindra (Johanson, 1997a).

Description

Headshield (Figs. 3–11). The premedian (PrM, Fig. 10E,H) is longer than wide (mean L/W ratio = 1.04), with the rostral margin wider than the orbital (mean ratio = 2.10). Internally, the lateral margins kink slightly inwards just below the rostral margin. An elongate roughened area is present along the midline of the internal surface of the premedian, in the anterior half of this plate.

The orbital fenestra (fe.orb, Fig. 3A) is wider than long (mean L/W = 0.55). Internally (Fig. 10A,B,D), the suborbital fenestra (fe.sorb) is smaller than the orbital fenestra (Fig. 5B). The preorbital recess (prh) is trifid, with three well-developed extensions (Figs. 4B, 7A–C, 8E, 9A–C, 9E). The borders of the otico-occipital depression (ood, Fig. 10A,B,D) are sharply defined by the paramarginal crista (cr.pm), and the anterior postorbital processes (pr.po) extend well beyond the anterior margin of the suborbital fenestra. The postorbital cristae (cr.pto) are well developed and extend onto the internal surface of the nuchal plate.

The pineal plate (P) is small and roughly rectangular (Fig. 5C), with reduced posterolateral corners. The pit on the internal surface of the pineal is deep, occupying most of this surface. The rostral plate (R) comprises a long, rectangular base, with a thin protrusion extending anteriorly from the midpoint of the base. This protrusion separates the nasal openings so that the rostral has the shape of an inverted "T". Large, rounded sclerotic ossicles (scl) are present, but usually broken. The postpineal (PP, Fig. 3A) is wider than long (mean L/W ratio = 0.83) with a rounded anterior margin that extends only slightly anteriorly into the orbital fenestra (Figs. 3A,D, 10A,B,G,H). Internally, a median ridge (mr, Fig. 10B) separates two large, rounded pits (g) that dominate the internal surface of the postpineal.

The lateral plate (L, Fig. 10D,E) was not measured due to damage along its lateral margin. Internally, a moderately large, shallow pit (p) is positioned just anterior to the narrowest part of the spiracular groove (Fig. 5C). The spiracular groove (spg) is long and shallow. It is widest at the lateral margin of the headshield, narrows abruptly at the pit, then widens gently again. The medial portion of the spiracular groove extends well beyond the anterior postorbital process, and appears to abut against the lateral protrusion of the preorbital recess. The anterior and posterior crests (cr1, cr2, Fig. 10A) of the spiracular groove do not fade medially, but are sharply developed along their entire extent. The anterior attachment for the submarginal (a1SM) is best preserved on AM F.100843 (Fig. 5C), where it is a strongly developed, transverse structure, bordering the anterior crest of the spiracular groove. At the mesial end of the anterior attachment, the anterior spiracular crest bends posteriorly towards the preorbital recess. The anterior submarginal attachment is separated from the more anterior prelateral attachment (a.PrL, Fig. 5C), which is small, oval-shaped and oriented laterally or postero-laterally. The posterior attachment for the submarginal (a2SM) is a single, elongate structure (Fig. 8C), widest anteriorly, narrowing posteriorly. The attachment extends from the midpoint of the postmarginal plate (PM, Fig. 8C) to the posterior spiracular crest, but does not extend anteriorly across the spiracular groove. The prelateral plate (Pr.L, Fig. 9D) is small and rounded, with a deeply incised sensory groove externally. No infraprelateral (e.g., Young, 1984: fig. 1) was observed.

Because the headshield is frequently preserved in articulation with the trunkshield, the paranuchal trochlea (pnt) on the internal surface of the paranuchal plate (PNu, Fig. 10B) is rarely observed. However, on AM F.101270 (Fig. 8C), these trochlea are elongate and narrow, extending the length of the paranuchal along the transverse nuchal crista. They are widest medially, narrowing concavely to a point mesially and laterally.

The mean L/W ratio of the nuchal plate (Nu, Fig. 10A) is 0.73. Externally, the endolymphatic ducts (d.end) are small, rounded openings. Internally, the endolymphatic ducts are still small, positioned on either side of the large supraotic thickening (sot). The majority of the surface of the supraotic thickening is covered by a moderately deep pit. The transverse nuchal crista (cr.tv) is well developed. Posterior to this, the median occipital crest of the headshield (cro, Fig. 10B) is well developed and sometimes divided, so that there are paired insertion areas for the levator muscles (fm). The lateral insertion areas dominate this area, and in one large specimen, AM F.100843 (Fig. 5C), these are very deep, but this may be related to the size of the individual or less flattening of the specimen. The postmarginal plate is roughly diamond-shaped. The widest lateral point (and the widest part of the headshield) is approximately in the middle of the postmarginal.

The submarginal plate (SM, Figs. 4A,D, 8, 9, 10B–G, 11C) is preserved on a small number of specimens, both in internal and external view. The lateral margins of the headshield were often not well preserved, being either flattened, damaged or difficult to prepare. Thus, the number of describable submarginal plates is low relative to the large number of individuals of *Bothriolepis yeungae* preserved in the fauna. Only one specimen thus far (AM F.100891, Fig. 4A,D) clearly shows the submarginal in external view. Six others (Figs. 8A,B,D,E, 9A–C,E) preserve the internal view. Although the number of preserved plates is low, they show an unusual morphology, as described below.

The submarginal plate is long, low anteriorly and high posteriorly. In external view the plate has a teardrop appearance, with a blunt anterior edge where it contacts the prelateral. The posterior submarginal attachment (ad2, Figs. 9B, 10C,D) is a raised, elongate, oblique area, situated

at approximately one-third the plate length. Anterior to this the plate lowers dramatically, marking the position of a wide, open notch (N, Fig. 10C) between the posterior and anterior (ad1) articular processes of the submarginal (Figs. 8A,B, 9A,B, 10A–C, 11C). The latter process is low, and well separated from the posterior process by the wide notch. This morphology is not believed to be due to damage because it is present in all those specimens where the submarginal is preserved (e.g., Fig. 9A,B,E). Furthermore, on AM F.100904 (Figs. 8A,B, 10B,C), the anterior portion of the submarginal rests on or nearly on the anterior submarginal attachment of the lateral plate, so that very little if any is missing. A large, roughened oval surface is present along the ventral margin of the submarginal (a.AVL, Fig. 10C), representing the contact area between the submarginal and the anterior ventrolateral plate. A comparison of this submarginal to those figured for other species of *Bothriolepis* and the antiarch *Nawagiaspis wadeae* Young, 1990, and a reconstruction of the internal surface of the headshield is presented in Fig. 11J.

The suborbital plates (SO) are preserved in life position in external (Figs. 7D, 10A, 13A) and internal views (Fig. 13D). The overall shape is rectangular with more prominent posterolateral corners. The lateral margin is somewhat concave down to this latter corner. The suborbital pair meet dorsomesially, becoming separated ventrally due to the oblique mesial margins of the plates. The ventral margin of the suborbital, best preserved on AM F.101232 (Fig. 13A), appears to be smooth, lacking denticulation. The ventral third of the suborbital is unornamented, and separated from the ornamented portion by a strongly developed ridge (r, Fig. 10A) running to the anterodorsal corner. The sensory canal (ifc3) runs ventrally from near the mesial margin of the dorsal edge, just offset from the midline of the plate, then bends laterally at the strongly developed ridge. The canal runs to the lateral edge of the suborbital, widening near this edge.

The only specimen thus far preserving the internal surface of the suborbital is AM F.100803 (Fig. 13D). This surface is dominated by a strong transverse ridge (tr) which begins near the dorsomesial margin, extends ventrally for a short distance, then curves to continue laterally to the edge of the plate. This ridge is located in approximately the centre of the plate and varies in height along its length, being highest in the middle and becoming lower laterally. The lateral third of the ridge is very low and appears closely applied to the surface of the suborbital. This morphology is similar to that described for *Bothriolepis* sp. from Gogo (Young, 1984) and *B. canadensis* (Stensiö, 1948).

Remnants of the anterior portion of the S-shaped infragnathals (Ifg, Fig. 13D) are preserved at the ventral margin of the internal surface of the suborbital, as curved structures wider laterally, narrowing to a point medially. There appears to be a second surface below and confluent with that just described. The now-flattened space between these two surfaces represents the groove along the ventral surface of the infragnathal, as described for *Bothriolepis* sp. from Western Australia (Young, 1984). The posterior portion of the infragnathal is missing, due to breakage at what would have been the thinnest part of the S-shaped infragnathal.

Sensory lines on the external surface of the headshield (ifc1, ifc2, cir, csl, socc, Fig. 10E,F,H) are similar to those found in other species of *Bothriolepis*.

Trunkshield (Figs. 3–10, 13–17). The mean L/W ratio of the anterior median dorsal (AMD) is 1.03. Externally (Fig. 10E–H), the highest point of the trunkshield is the dorsal median ridge (dmr, Fig. 10H) which runs from just anterior to the middle portion of the AMD (dma, the tergal angle, Fig. 10E) to the posterior margin of the posterior median dorsal. The posterior oblique dorsal sensory line groove (dlg2) runs posterolaterally across the AMD and mixilateral plates (MxL) from the tergal angle. Internally (Figs. 5B,D, 8A, 9A, 14F, 15C–F, 16B,E, 17F,G), the postlevator thickenings (alr, Fig. 17F) are low and oblique, grading gently into the surrounding plate. The postlevator crista (cr.pl) are sharp and high, and are separated from the anterior margins of the postlevator thickenings, extending instead into the posterior portion of the levator fossa (f.retr). The posterior levator processes (pr.pl) are moderately developed. The median ventral ridge (mvr) extends anteriorly from the anterior ventral pit of the dorsal wall of the trunkshield (pt1) into the shallow, triangular levator fossa, the latter being more strongly developed on some specimens (Fig. 5D) than others (Figs. 14F, 15C–F). This is not considered to be an important taxonomic difference and may be related to the overall size of the individual. The anterior ventral pit is located at the confluence of the postlevator cristae, and is long, open and narrow. The postlevator cristae issue from the midpoint of the pit (Figs. 5B, 15C), or from its anterior edge (Figs. 5D, 14F). The median ventral ridge extends posteriorly from this pit, splitting to form a median walled groove (grm, Fig. 17G) at approximately one-half the length of the AMD, which then fades before the posterior margin of this plate. Overlap areas for the ADL (cf.ADL, Fig. 17F) are moderately wide, as in other species of *Bothriolepis*.

The posterior median dorsal (PMD) is bell-shaped externally, with well-developed lateral corners and a small, triangular posteriormost corner (pa, Figs. 3A, 10G, 17B,E). Internally (e.g., Fig. 14C,D,G), the median groove (grm, Fig. 17B) continues posteriorly from the AMD, but lacks the thin walls of this groove, and is instead more like a linear depression stretching to the posterior ventral pit (pt2). At the posterior margin of the PMD, the *crista transversalis interna posterior* (cr.tp) forms a strongly developed, rounded ridge that continues onto the mixilateral plate. The posterior marginal area (pma, Fig. 17E), between the posteriormost margin and the *crista transversalis interna posterior* is narrow laterally and wider medially. The posterior ventral pit sits just anterior to the *crista transversalis interna posterior*, connected by a short, low ridge, the posterior ventral process (prv2). In some specimens (Fig. 14C,F), the posterior ventral pit is covered and so more like a high ridge. A faint ventral tuberosity (tb, Fig. 17B,E) surrounds the posterior ventral pit. Lateral to the *crista transversalis interna posterior* and following the line of this ridge are the lateral processes (prl). The anterior and lateral overlapping areas of the PMD (cf.AMD, cf.MxL) are wide.

The dorsal lamina of the anterior dorsolateral plate (ADL) is preserved on most specimens, but the lateral lamina is usually flattened and hidden from view. On AM F.101276 (Fig. 13C) and AM F.101277 (Fig. 13F), the ADL is less crushed, and the anterolateral surface can be seen (Fig. 13F). The *processus obstans* (pro, Figs. 10F,H, 13F) is very large and rounded, which can also be seen in dorsal view, where it articulates with the postmarginal and paranuchal (Fig. 5A). The main lateral line groove (lcg, Fig. 13F) runs across the middle of the *processus obstans* where it turns upward to cross on to the headshield. The ornamented angle (pnoa) is elongate and strongly developed. Below this, the two crests defining the articular fossa, the supra- and infraarticular cristae (crs, cri), are also strongly developed, and the articular fossa (f.art) contacting the paranuchal trochlea is deep and concave. The *crista transversalis interna anterior* (cit) is the dominant feature of the anterior articular area, being large and triangular with a rounded posterior margin. The overlap area for the AMD (oa.AMD, Fig. 13F) is widest anteriorly, where the AMD possesses small lateral extensions. It then appears to narrow posteriorly.

Several anterior ventrolateral plates (AVL) are preserved, showing internal and external surfaces. The ventral lamina is preserved (Fig. 13A,B), but the lateral surface is rarely seen, again due to flattening (e.g., AM F.100891, Figs. 4D, 10F). On the latter specimen, the lateral lamina is not visible in its entirety, but the following features can be noted. The lamina is narrow above the area of pectoral fin attachment, and the anterodorsal corner appears to be low, although the lateral lamina of the AVL may have slipped under the ventral margin of the ADL. The prepectoral corner (prc) is not present on this specimen (Fig. 4A), but a small corner is visible on others (Fig. 13A). The AVL continues anteriorly from this point as a narrow elongation overlapped by the submarginal.

As noted above, articulation of the pectoral fin to the AVL obscures certain features of the fin attachment on the AVL, for example, the *margo limitans* and the *fossa articularis pectoralis*. However, on AM F.100891 (Figs. 4D, 10F), the brachial process (pbr, Fig. 10F) is visible, being large, rectangular, with a large funnel pit (fp). The process faces posteriorly or slightly posterolaterally. This is also observed on AM F.100886 (Fig. 16D), where the anterior dorsal and ventral muscle insertions (a.sup, a.inf) are visible. These are positioned above and below the funnel pit and are elongate, curved and deep. The *pars pedalis* (pe, Fig. 4E) is short and extends horizontally. The axillary foramen (f.ax, Fig. 14H) behind the brachial process is not visible externally (e.g., Fig. 4D), again due to the attachment of the pectoral fin. However, one specimen (Fig. 14E,H) preserves an AVL with an articulated pectoral fin. The lateral lamina of this AVL is mostly absent, but a small portion is preserved near the anterior part of the pectoral fin. In internal view, a large, elongate opening is visible in this portion of the lateral lamina, representing the axillary foramen (cf. Young & Zhang, 1992: fig. 8A). This foramen is surrounded anteriorly by a wide, raised ridge. Part of the medial opening of the pectoral fin is visible, and some type of material is visible at this opening. This may be a portion of the endoskeletal unit inside the fin (Stensiö, 1948, 1969), or it may simply be sediment infill.

The anterolateral corner of the subcephalic division of the ventral lamina of the AVL (c.al, Fig. 17A) is distinct, and the anterior margin contacting the semilunar plate is long (m1, Fig. 14A). Other overlapping areas (cf. AVL, cf. MV, cf. PVL, Fig. 17A) are visible on the internal surface of the plate and are wide and well developed. The *crista transversalis interna anterior* (cit, Fig. 17A,D) is developed as a high, thin ridge running at an oblique angle across two-thirds the width of the anterior portion of the plate.

The dorsal lamina (dlm, Fig. 17C) of the mixilateral plate is nearly twice as wide as the height of the lateral lamina (Figs. 13G, 15G). The overlap surface for the PMD (oa.PMD, Fig. 17C) is wider posteriorly, narrowing anteriorly. The overlap surface for the ADL (oa.ADL) is arrow-shaped, with the dorsal portion being narrower than the lateral portion. On the lateral lamina, the overlap for the posterior ventrolateral (oa.PVL) is very narrow anteriorly, widening rapidly posteriorly until it occupies the majority of the lamina. The overlap area ends at this point, and posterior to this is a relatively wide, triangular posteroventral ornamental angle of the mixilateral (cu). The main lateral line groove (lcg) runs across the midline of the ornamented portion of the lateral lamina and is thus relatively widely separated from the dorsolateral ridge of the trunk armour (dlr) anteriorly, but rises towards this ridge posteriorly. Here, the lateral line groove curves ventrally to meet and run posterior to the dorsalmost margin of the PVL overlap area.

The lateral lamina of the posterior ventrolateral (PVL) is not well preserved, but the ventral lamina can be observed in some specimens (Fig. 13A,B). The ventral lamina is broadest anteriorly, beginning to narrow just at its posterior half. The lamina narrows sharply at this point to the posterior margin, which is small and slightly rounded. The median ventral plate (MV) is visible in AM F.101232 and AM F.101261 (Fig. 13A,B), where it is moderately large relative to the surrounding plates, as in most species of *Bothriolepis*.

Pectoral fins. The pectoral fins are frequently found articulated to the AVL and often fully adducted to the trunkshield so that their medial face is not visible. As well, the fins are frequently crushed or broken. The fin itself is long, extending beyond the posterior margin of the trunkshield (Figs. 3, 6A,C). The fin is hinged distally, and the distal portion of the pectoral fin is approximately one-third the length of the proximal portion. The lateral marginal plate 2 (Ml2, Figs. 4E, 17A,D) is the dominant plate of the proximal pectoral fin, wrapping around the lateral margin of the fin and extending on to the ventral surface. The lateral margin is sharp, not rounded, and is lined with a series of small protrusions (Fig. 3A).

The two most proximal plates dorsally (Cd1) and ventrally (Cv1) articulate with the brachial process on the AVL (Fig. 4E). The articular areas of these plates are narrow, elongate areas (ar3d, ar3v, Figs. 10F, 13B), separated from the rest of the ornamented plate by a thin,

unornamented section. On AM F.100886 (Figs. 16C, 17D), the internal articular area of Cv1 can be seen as a roughened, striated surface (ar1v). The Cd1 and Cv1 articulate closely with the brachial process (e.g., Fig. 4E), although the plates themselves are separated anterolaterally around the *pars pedalis* (pe) by a narrow, U-shaped area. This area is wider than the *pars pedalis*, suggesting that the fin could move dorsal and ventral relative to the trunkshield to some degree (Young & Zhang, 1992). Just posterior to this area, the Cd1 and Cv1 articulate for a very short distance, then are separated by the Ml2, which comes to a rounded point in this area.

AM F.101249 and AM F.100900 preserve the pectoral fin in internal view (Fig. 14B,H), and show that Cd1, Cv1 and the mesial marginal plate 1 (Mm1) formed a rounded proximal opening of the pectoral fin. This opening is intimately associated with the axillary foramen although the posterior extent of this foramen is not known.

In contrast to the sharp lateral margin, the mesial face of the pectoral fin forms a low, flat wall that allows the fin to be held flat against the trunkshield when fully adducted (Fig. 14H). The Mm1 is elongate, forming a narrow lip to separate Cd1 and Cv1 (Fig. 14B). The Mm1 extends posteriorly to contact the Mm2, which wraps around from the dorsal surface. The Mm1 is only approximately two-thirds as long as the Mm2. The overlap relationship between the mesial and ventral plates of the fin is a potentially important taxonomic character for *Bothriolepis*, but unfortunately only visible on one specimen of *B. yeungae* to date (Fig. 14B). On this specimen, the Mm1 overlaps the anterior margin of the Mm2, which is slightly concave. A small portion of the Cv1 and Cv2 plates are visible just below these mesial marginal plates, and all four appear to meet at a cross-shaped junction just dorsal and to the left of the line marking Cv1 in Fig. 14B. Therefore, these four plates all contact another at a point, such that the Cv2 and Mm1 do not overlap. Other more distal plates of the pectoral fin (Cd2, Cd4, Cd5, Ml4, Ml5, T, Figs. 10G, 17D), are as in other species of *Bothriolepis*.

Posterior body and fins. The body of *Bothriolepis yeungae* posterior to the trunkshield is very rarely preserved in the Canowindra fauna, and was probably not scale-covered. By contrast, the post-trunkshield body of *Remigolepis walkeri* was scale-covered, and is very commonly preserved (Johanson, 1997a). One specimen of *B. yeungae* (AM F.105545) preserves the external mould of a long, elongate body (approximately 1.2 times the length of the head and trunkshield) in dorsal view, but little additional morphological information can be obtained. No scale impressions are preserved on this specimen, and there is no indication of dorsal or caudal fins. Otherwise, rare patches of faint lepidotrichia-like elements have been observed in the Canowindra fauna, and may belong to *B. yeungae* (A. Ritchie, pers. comm.), but do not occur in clear association with specimens of *Bothriolepis*. Trunk scales also appear to be absent in *B. canadensis* (Stensiö, 1948), but are strongly developed in the Victorian species *B. gippslandiensis*, *B. cullodenensis* and *B. fergusoni* (Long, 1983; Long & Werdelin, 1986), particularly the ventrolateral scales.

Since the morphology of the caudal fin cannot be interpreted from the specimen discussed above, the reconstruction of *Bothriolepis yeungae* presented in Fig. 18 is based on *B. canadensis* (Stensiö, 1948). A lateral reconstruction is not presented due to flattening and crushing of specimens.

Comparisons to other species of *Bothriolepis*

Bothriolepis yeungae is characterised by the presence of a submarginal in which the low anterior process is well separated from the more typical posterior process by a wide, rounded notch (Fig. 11C). This appears to be unique within *Bothriolepis*, however, it should be noted that no disarticulated submarginal plates have been observed for *B. yeungae*, so that the specimen shown in Fig. 11C is not shown strictly in mesial view. Other plates in Fig. 11 are seen in direct lateral or mesial view, but this is not felt to be an overwhelming problem when comparing these to *B. yeungae*. In other species of *Bothriolepis* (Fig. 11A,D–I) and antiarchs like *Nawagiaspis* (Fig. 11B), the anterior process of the submarginal is raised and more similar in height to the posterior, while the notch between the processes is smaller and more closed. Exceptions to this are *B. cullodenensis* (Long & Werdelin, 1986: fig. 5D), *B. cullodenensis* (Long & Werdelin, 1986: fig. 11A; Fig. 11I) and one specimen of *B. canadensis* (Stensiö, 1948: fig. 105B; Fig. 11D) in which the anterior submarginal process is also reduced in height. However, the submarginal in front of the notch is very short, relative to the more elongate process in *B. yeungae* (Figs. 10B,C, 11C). Additionally in *B. cullodenensis*, there is a long, roughened area extending posteroventrally from the anterior submarginal process which Young & Zhang (1992: 459) suggest may have held cartilage attaching to the anterior postorbital processes of the braincase, as in other placoderms. In *Bothriolepis*, attachment between the submarginal and lateral plates is direct, and this cartilage is usually absent (Young, 1986). In fact, Young & Zhang (1992) imply that the anterior submarginal process may have been absent in *B. cullodenensis*, a plesiomorphic condition for *Bothriolepis* and unlike the condition in *B. yeungae*. As well, no roughened area for cartilage attachment is present on the internal submarginals of *B. yeungae* (Figs. 8A,B,D,E, 9A–C,E).

Relatively few synapomorphies designating clades of species within *Bothriolepis* have been identified, and these have tended to be more inclusive clades, containing several species. Thus, relationships of species within these clades have been less well elucidated. The most recent attempts to summarise the phylogenetic relationships of various species of *Bothriolepis* were made by Long (1983) and Young (1988; Fig. 12). In the former, the structure of the cladogram was based on changes in the shape of the preorbital recess of the headshield, from a plesiomorphic semicircular form through to a derived trifid recess. Young (1988) expanded on this, providing additional synapomorphies for a group characterised by a pentagonal preorbital recess, including the presence of a strong, transverse anterior submarginal attachment on the lateral plate, separated from the attachment for the prelateral plate.

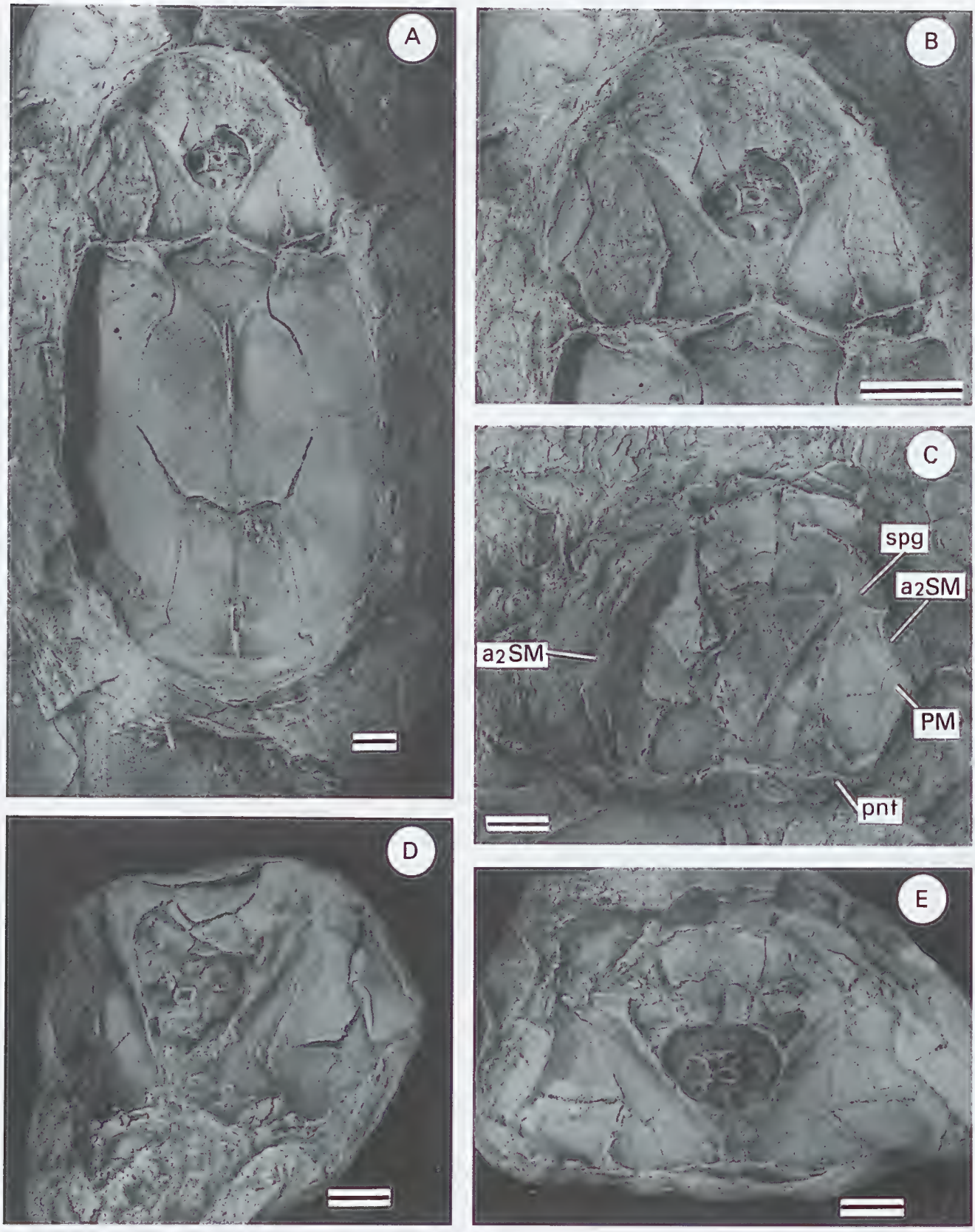

Figure 8. *Bothriolepis yeungae* n.sp. A, AM F.100904, internal view of head and trunkshield; B, AM F.100904, closeup of internal view of headshield; C, AM F.101270; D, AM F.100894; E, AM F.100888; C–E, internal view of headshield. Scale = 1 cm.

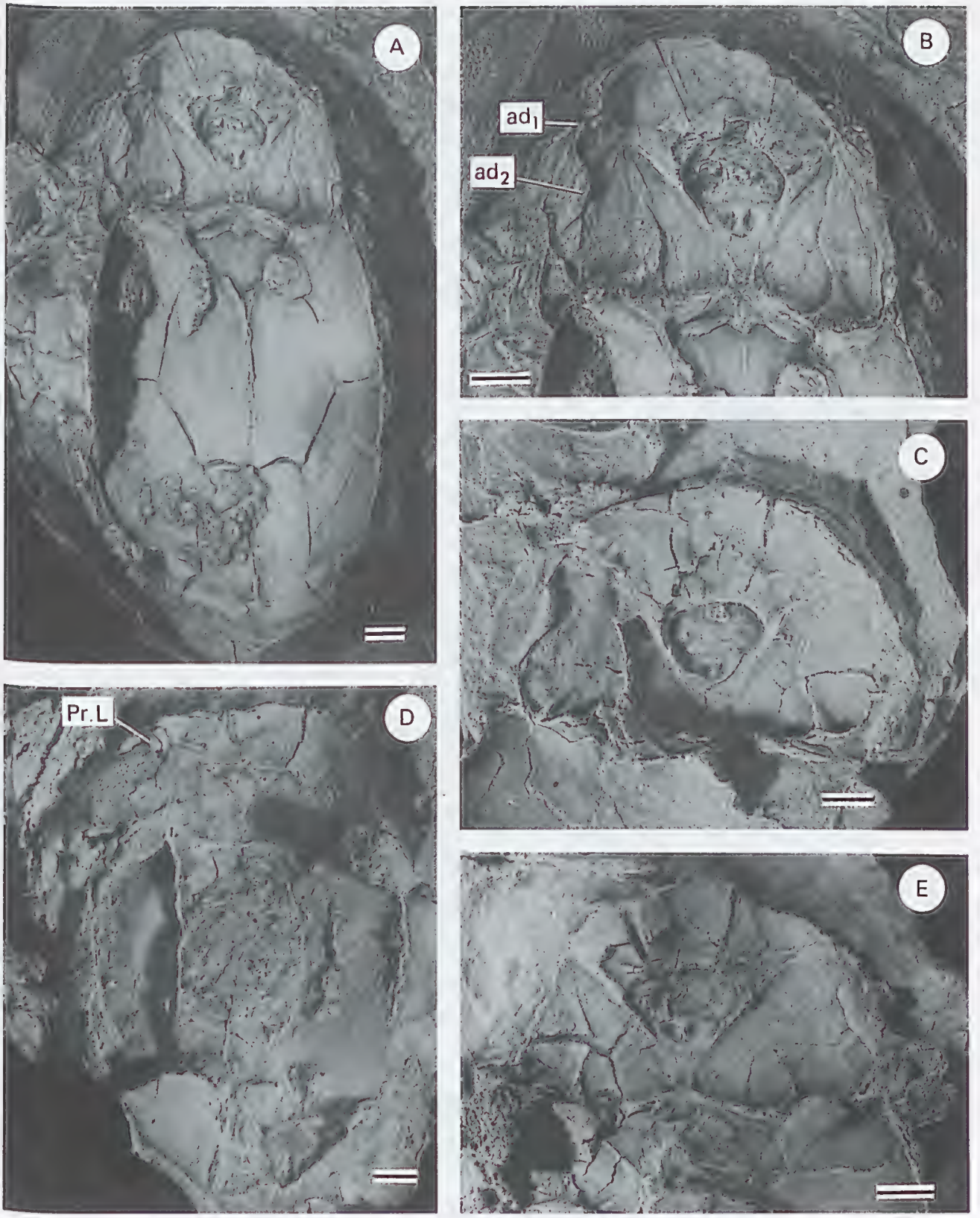

Figure 9. *Bothriolepis yeungae* n.sp. A, AM F.102398, internal view of head and trunkshield; B, AM F.102398, closeup of internal view of headshield; C, AM F.100844, internal view of headshield; D, AM F.100899, internal view of head and trunkshield; E, AM F.101273, internal view of headshield. Scale = 1 cm.

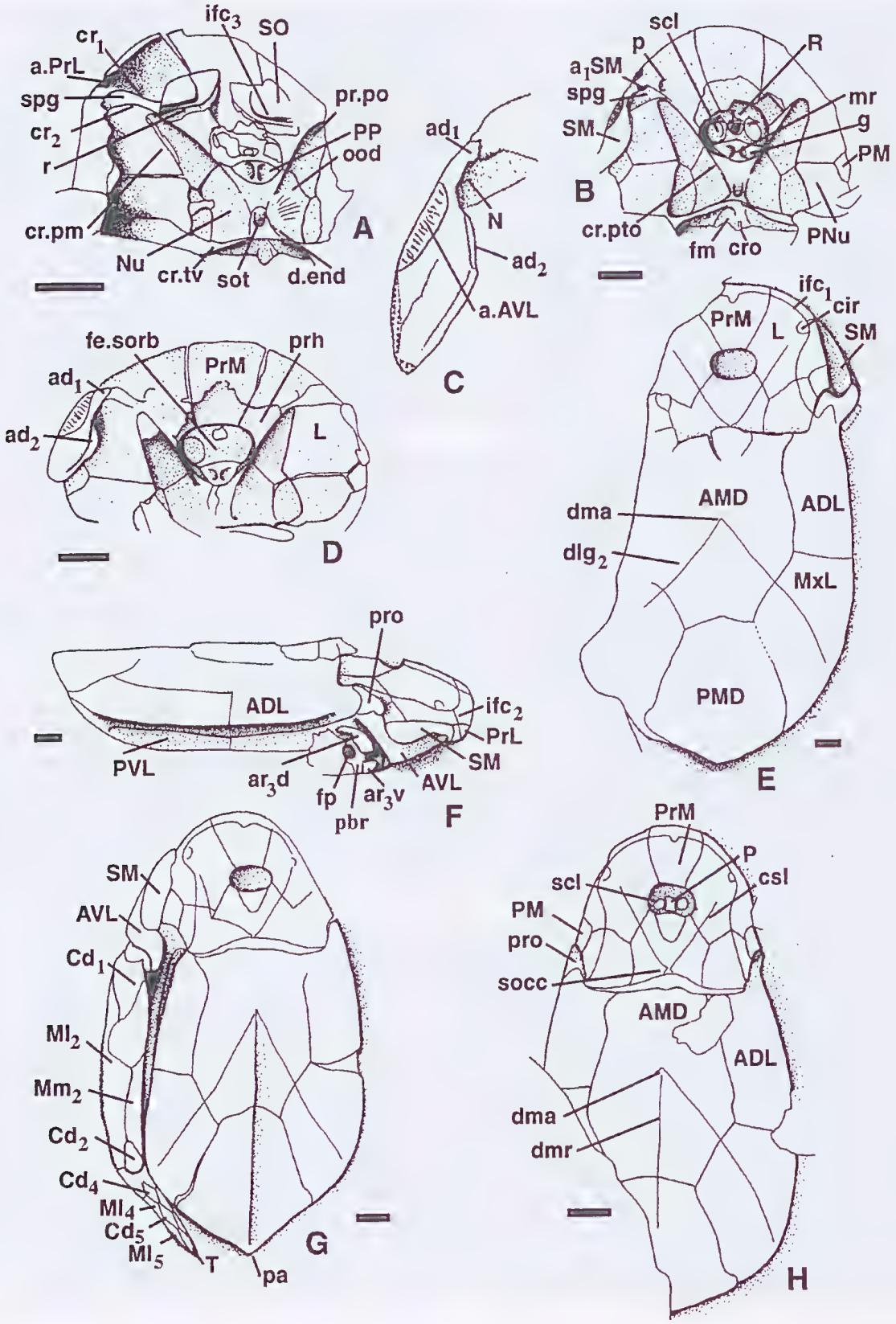

Figure 10. *Bothriolepis yeungae* n.sp. A, AM F.100842, internal view of headshield with suborbital plates; B, AM F.100904, internal headshield; C, AM F.100904, detail of right submarginal plate; D, AM F.100844, internal view of headshield; E,F, AM F.100891; G, AM F.101247; H, AM F.100802a, all dorsal view of head and trunkshield, except F, lateral view. Scale = 1 cm.

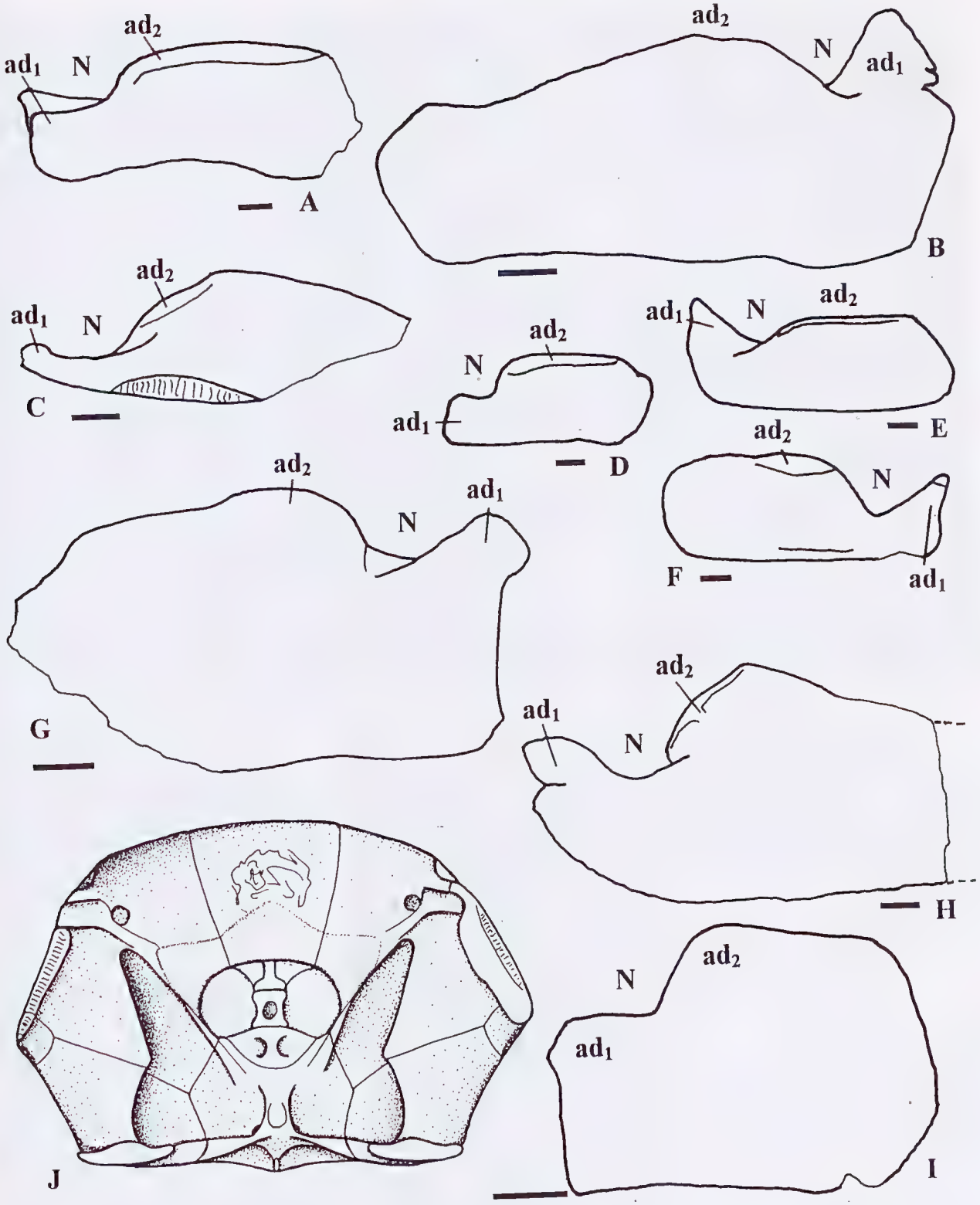

Figure 11. A–I, outlines of submarginals of various species of *Bothriolepis*, and of *Nawagiaspis*. A, *Bothriolepis canadensis*: Stensiö, 1948; B, *Nawagiaspis wadeae*: Young, 1990; C, *Bothriolepis yeungae* n.sp. Note that while other submarginals are shown in lateral view, that of *Bothriolepis yeungae* n.sp. is seen in a slightly oblique view, as preserved attached to the headshield (see text for further discussion); D,E, *Bothriolepis canadensis*: Stensiö, 1948; F, *Bothriolepis obruschewi*: Karatajute-Talimaa, 1966; G, *Bothriolepis* sp. from the Gogo Formation, Western Australia (Young, 1984); H, *Bothriolepis macphersoni*: Young, 1988; Young & Zhang, 1992; I, *Bothriolepis cullodenensis*: Long & Werdelin, 1986; J, *Bothriolepis yeungae* n.sp. Reconstruction of internal headshield, slightly flattened to show attachment of submarginal plate.

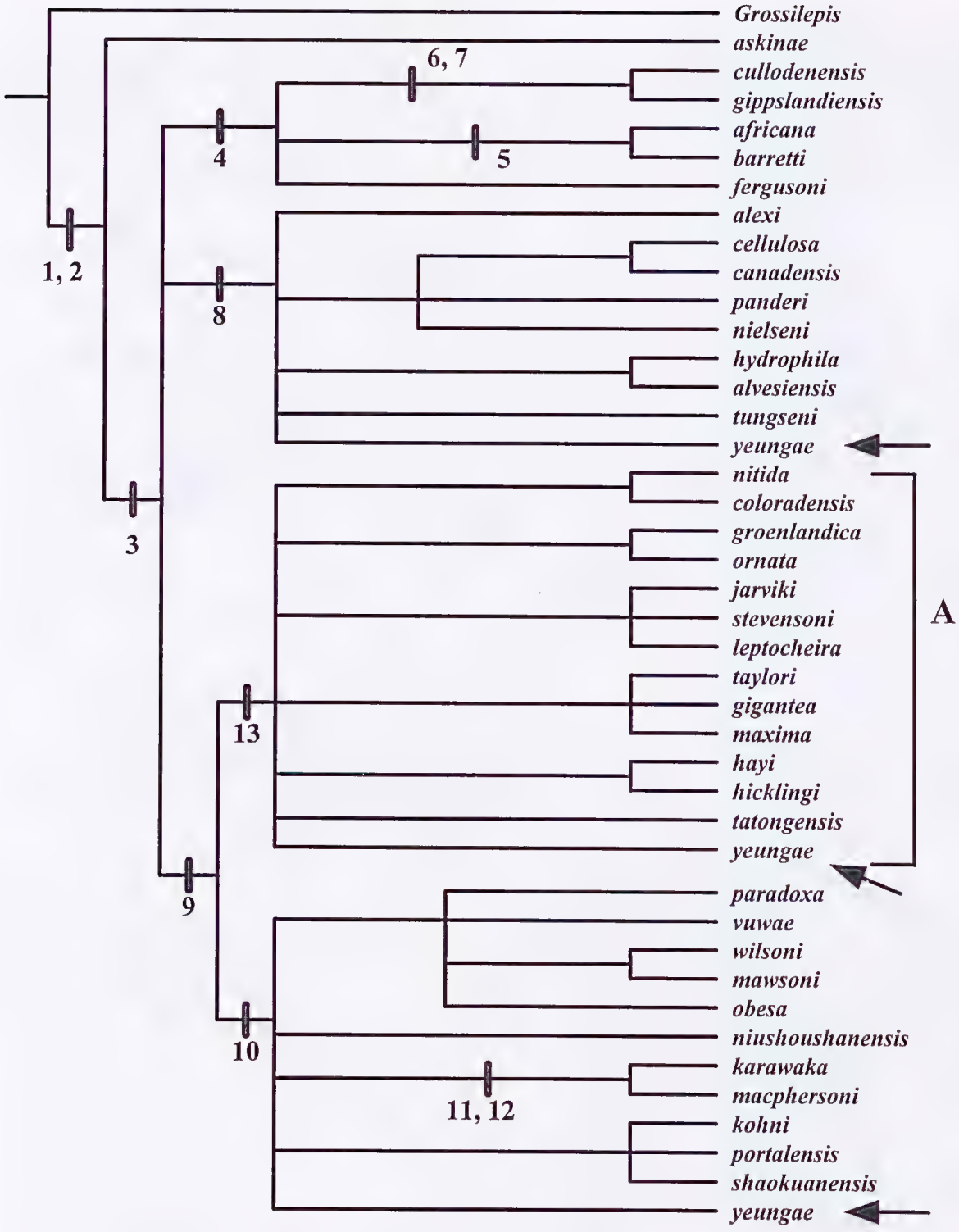

Figure 12. Cladogram of *Bothriolepis*, adapted from Young (1988: fig. 68). Note multiple position of *B. yeungae* on this cladogram, denoted by arrows. Synapomorphies are as follows (letters in brackets indicate characters designated by Young [1988]): 1—reticulate ornament in juveniles and adults (a); 2—AMD in adults broadest across lateral corners, and MxL broadest through its dorsal corner (b); 3—lateral corners on AMD appear early in ontogeny (c); 4—enlarged lateral pit (d); 5—trilobate prelateral recess (e); 6—trunk armour with pronounced median dorsal crest (f); 7—short, deep, SM plate (g); 8—point contact between Cv1, Cv2, Mm1 and Mm2 (h); 9—pentagonal preorbital recess (i); 10—anterior submarginal attachment on lateral plate a transverse ridge (j, modified from Young, 1988); 11—separate ventrally facing attachment surface for the prelateral on the lateral plate (m); 12—*crista transversalis interna anterior* transversely oriented on ventral lamina of AVL (n); 13—trifid preorbital recess (r).

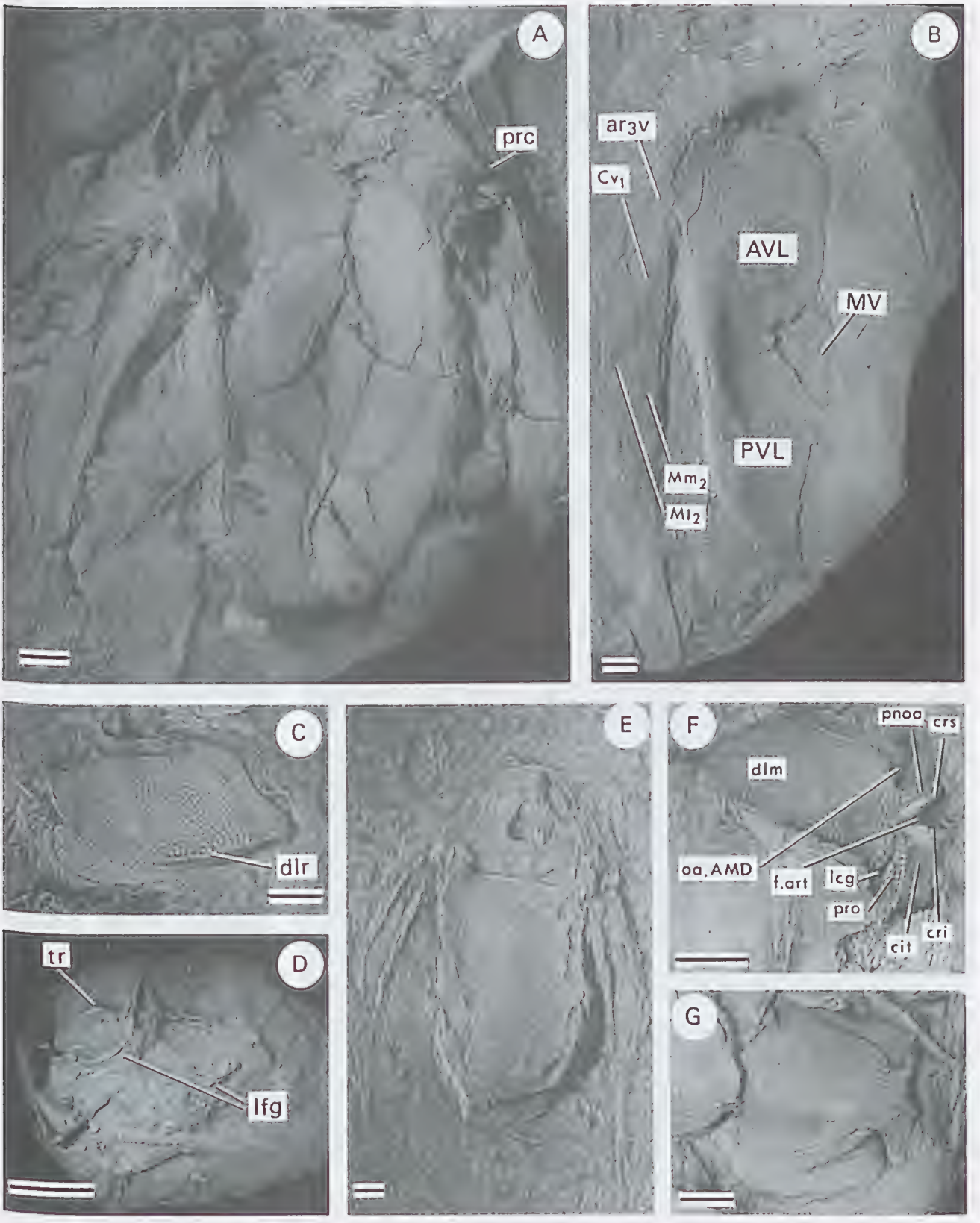

Figure 13. A, AM F.101232; B, AM F.101261; A,B, both ventral view of trunkshield and pectoral fin; C, AM F.101276, dorsolateral view of ADL; D, AM F.100803, internal view of suborbital plates; E, AM F.102399, dorsal view of head, trunkshield and pectoral fin; F, AM F.101277, anterolateral view of ADL; G, AM F.100841, lateral view of mixilateral plate. Scale = 1 cm.

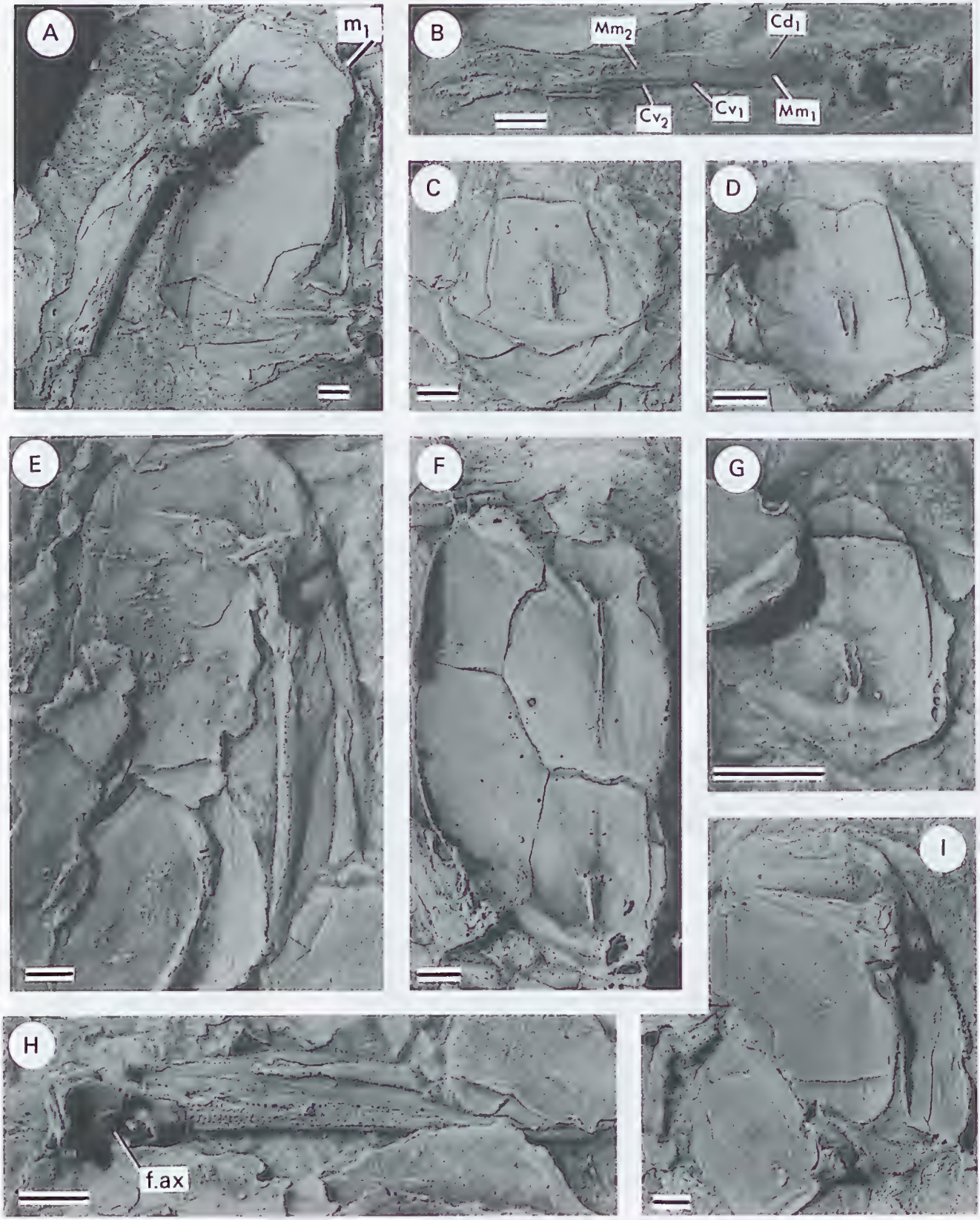

Figure 14. *Bothriolepis yeungae* n.sp. A, AM F.101249, internal view of AVL with partial pectoral fin; B, AM F.101249, closeup of medial pectoral fin; C, AM F.100838, internal view of PMD; D, AM F.100839, internal view of PMD; E, AM F.100900, internal view of AVL with partial pectoral fin; F, AM F.100898, internal view of partial trunkshield; G, AM F.101855, internal view of PMD; H, AM F.100900, closeup of medial pectoral fin and part of internal pectoral fin attachment; I, AM F.100840, internal view of AVL with partial pectoral fin.

Figure 15. *Bothriolepis yeungae* n.sp. A, AM F.101609, internal view of AVL with partial pectoral fin; B, AM F.101251, internal AVL, AM F.101252, AM F.101253, external MVs; C, AM F.101241, internal view of AMD; D, AM F.101246, internal view of AMD; E, AM F.101244, internal view of AMD; F, AM F.101245, internal view of AMD; G, AM F.101255, external dorsolateral view of MxL; H, AM F.101256, internal view of PMD.

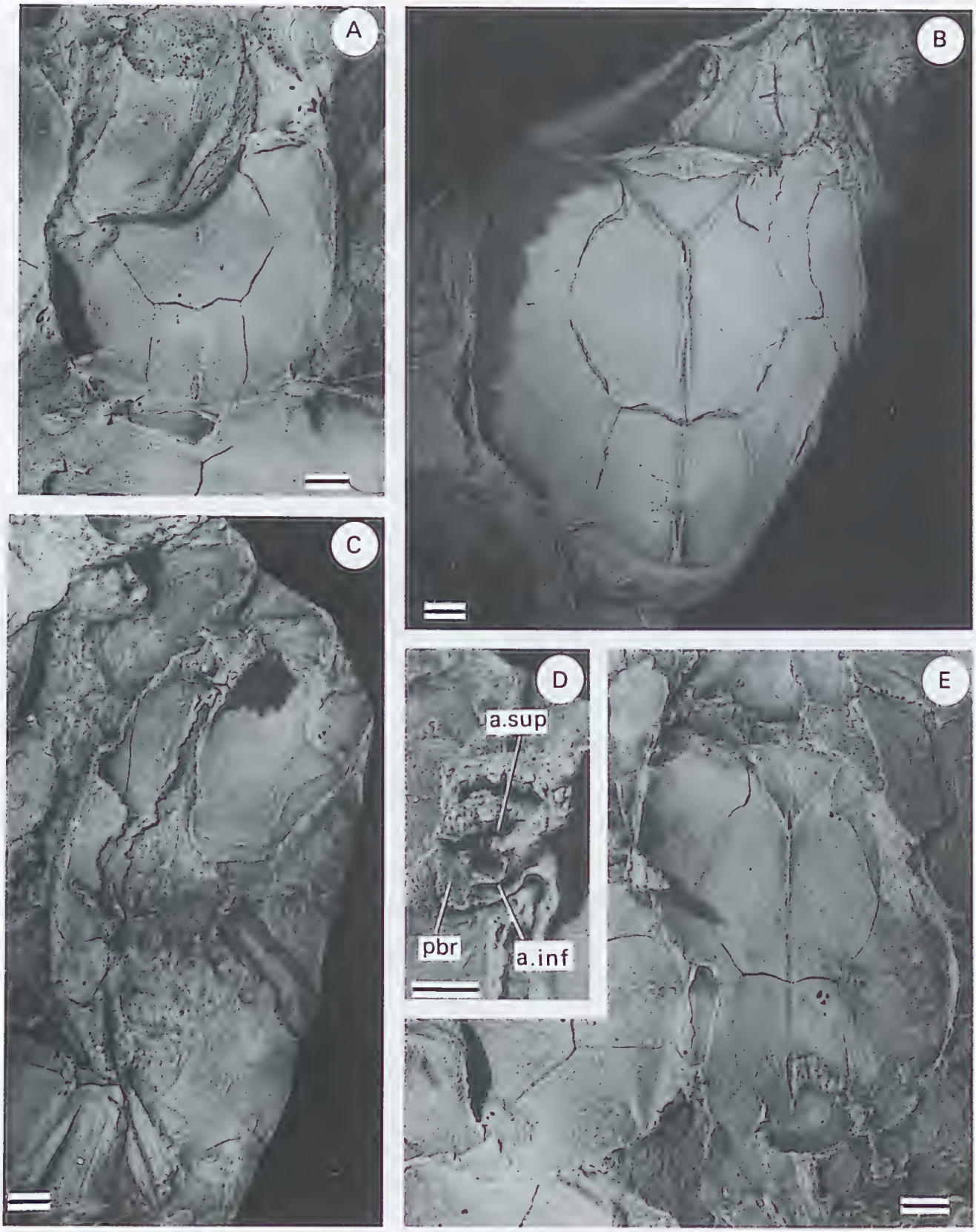

Figure 16. *Bothriolepis yeungae* n.sp. A, AM F.100897, internal view of trunkshield; B, AM F.101233, internal view of trunkshield and partial headshield; C, AM F.100886, internal view of AVL with pectoral fin; D, AM F.100886, closeup of brachial process; E, AM F.100896, internal view of trunkshield. Scale = 1 cm.

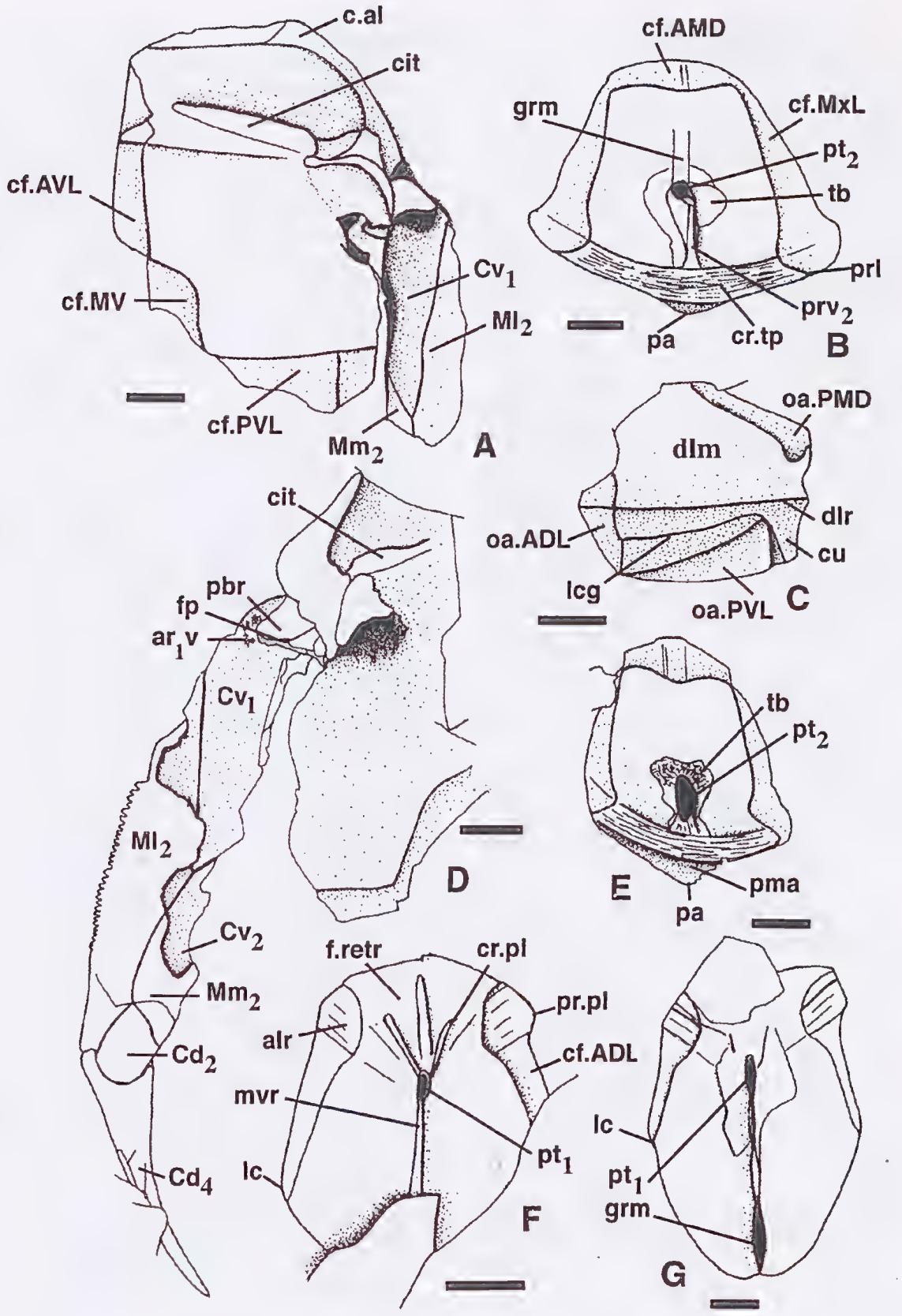

Figure 17. *Bothriolepis yeungae* n.sp. A, AM F.100840, internal view of AVL with pectoral fin; B, AM F.100838, internal view of PMD; C, AM F.100841, lateral view of mixilateral plate; D, AM F.100886, internal view of AVL with pectoral fin; E, AM F.100839, internal view of PMD; F, AM F.101241, internal view of AMD; G, AM F.100244, internal view of AMD. Scale = 1 cm.

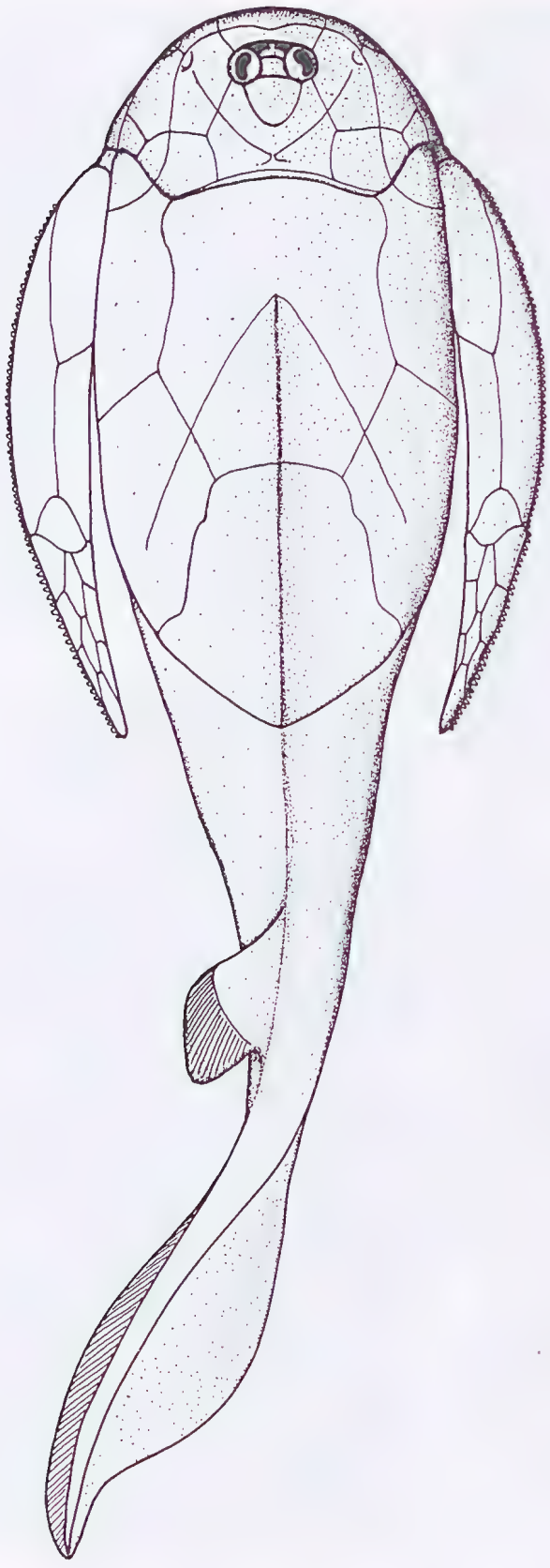

Figure 18. *Bothriolepis yeungae* n.sp. Reconstruction in dorsal view, based on specimens in Fig. 3; caudal fin morphology from *Bothriolepis canadensis* (Stensiö, 1948).

This also characterises *B. yeungae* (Fig. 12, character 10), although *B. yeungae* differs from these species in possessing a trifid preorbital recess.

In Young's cladogram, the trifid preorbital recess was a synapomorphy of a clade consisting of Northern Hemisphere taxa (clade A, Fig. 12, character 13). Among these, *Bothriolepis yeungae* is separated from taxa like *B. leptocheira* and *B. gigantea* (Miles, 1968) in possessing the strongly developed transverse anterior submarginal attachment and well-developed crests of the spiracular groove. These taxa, as well as *B. hayi*, lack the small pit on the internal surface of the lateral plate present in *B. yeungae*. *Bothriolepis maxima* (Stensiö, 1948: fig. 233) possesses a very small pit, but a weaker and more oblique anterior submarginal attachment, and what appears to be continuous anterior and posterior attachments for the submarginal around the spiracular groove. Additionally, the pit on the internal surface of the AMD is very large in *B. maxima* (Stensiö, 1948: fig. 238), and the pit on the internal surface of the PMD is distinctly anteriorly placed, as in *B. jarvki* (Stensiö, 1948: fig. 305). In *B. hicklingi*, the pit on the internal lateral plate is said to be broad and shallow (Miles, 1968: 108), although this is not visible on certain specimens (Miles, 1968, pl. 36, figs. 5, 10). Additionally, the PMD plate is unusual in possessing a large open pit on the internal surface, not connected to the *crista transversalis interna posterior* by a ridge. In *B. nitida* (Stensiö, 1948: 395), the ornament is very coarse, and the terminal segment of the pectoral fin is striated, appearing to lack the polygonal plates more characteristic of *Bothriolepis*.

The trifid recess type also occurs in *B. grenfellensis* from the Grenfell region of NSW (Johanson, 1997b), *Bothriolepis* sp. from the Jemalong fauna from Forbes, NSW, and *Bothriolepis* sp. from Gogo, Western Australia. However, *B. grenfellensis* lacks the separate, transverse anterior attachment for the submarginal seen in *B. yeungae*, instead possessing a small, oval attachment separated from the prelateral attachment by only a narrow groove. The anterior attachment for the submarginal in *Bothriolepis* from Gogo (Young, 1984) is more rounded still.

Within the groups possessing a semicircular recess, one clade is characterised by a point contact between Cv1, Cv2, Mm1 and Mm2, preventing overlap between the Cv2 and Mm1 plates (Young, 1988; Fig. 12, character 8), including taxa from Euramerica and South China. The pectoral fin of *B. yeungae* also shows this point contact, but differs from all species in this clade in the possession of a trifid preorbital recess.

The different synapomorphies from the cladogram of Young (1988) possessed by *B. yeungae* indicate that some of these must instead be homoplastic for *Bothriolepis*. Long *et al.* (1997: 266) imply that the morphology of the preorbital recess is the most important character in distinguishing clades of *Bothriolepis* species. However, all characters in a phylogenetic analysis should *a priori* be given equal weight, and difficulties in placing *B. yeungae* into clades recognised by Young (1988; see Johanson & Young, in press, for problems placing *Bothriolepis* from Nettleton's Creek, NSW) indicate that

certain morphological characters contradict phylogenies suggested by preorbital recess morphology. No attempt is made at this point to reanalyse the phylogenetic relationships of *Bothriolepis*, which will require a considerable and painstaking search for the qualitative characters necessary.

Therefore, it is presently difficult to identify the closest relatives of *Bothriolepis yeungae*. Of particular interest in this regard will be the morphology of *Bothriolepis* sp. from the nearby Jemalong fauna, placed in the same macrovertebrate zone as the Canowindra fauna by Young (1993). The *Bothriolepis* in each fauna have a trifid preorbital recess; as well, *Bothriolepis* occurs in association with *Remigolepis* and the dipnoan *Soederberghia* in both faunas. These comparisons will be part of a future work on the Jemalong fauna.

Palaeoecology of the Canowindra fauna

Certain observations that can be made with regards to the Canowindra fauna provide evidence as to the life and death of these fish, including: (*a*) the recovery of the fauna from a single bedding plane in the Mandagery Sandstone, with fish lying side by side rather than on top of one another; (*b*) the large number of fish crowded together on the rock slabs (Fig. 19B,C); (*c*) the excellent preservation of the fish (e.g., Fig. 3); (*d*) the preservation of the fish predominantly in life position, with dorsal surfaces upward.

The first observation indicates that the Canowindra fauna represents the remains of a Devonian palaeocommunity including fish that lived, interacted and died together. Time averaging (Walker & Bambach, 1971; Fürsich & Aberhan, 1990; Kidwell & Flessa, 1995; Olszewski & West, 1997), where plants and animals from different time periods can become concentrated or collected by biological or physical agents, is not believed responsible. Fürsich & Aberhan (1990) list various ways to recognise a time-averaged fauna, including evidence of physical transport of skeletal elements (e.g., disarticulation), or differences in preservation quality among the skeletal elements. The latter indicates that individuals from different times with different taphonomic histories have become mixed; neither this nor disarticulation is characteristic of the Canowindra fauna.

Additionally, individuals from different time periods can be accumulated by the winnowing of sediments, or if overall sedimentation rates are low. However, it is assumed that this type of accumulation would result in a thicker layer of fossils (e.g., a bone bed), which again, is not characteristic of the Canowindra fauna. Thus, the layer of fish in the Canowindra fauna comprises individuals living together and subsequently dying together during one restricted time period.

The second observation, crowding of a large number of fish on the rock slabs, is compatible with three scenarios: (*a*) loss of water habitat during dry conditions, forcing the fish to occupy a shrinking pool of water; (*b*) a mass kill of fish in water; (*c*) attritional death of fish in water, with subsequent accumulation and collection of individuals. The last scenario requires fish to die over an interval of time, potentially years, which contradicts the suggestion above that the Canowindra fish lived together and died within a short period. As well, accumulation of these individuals would require transport, which generally leads to disarticulation of skeletal elements or overturning of individuals. Disarticulation can be affected by degree of decay, where skin and flesh could hold bones, plates and scales together over some distance. Susceptibility to overturning can be influenced by morphology, where the flat-bottomed antiarchs may be more stable during transport. However, an example of physical agents collecting and overturning antiarchs may be seen in the assemblage of very large *Remigolepis* from near Eden, NSW. Here, several specimens (with fully articulated head and trunkshields) are closely spaced and almost entirely on their sides (pers. obs.). Additionally, the accumulation of over 3000 fish in the Canowindra fauna would require transport of individuals from over a wider area. It seems doubtful that so many fish could be transported over greater distances without a proportionately greater number being overturned or disarticulated in the process. In fact, the only distinct disarticulation of fish in the Canowindra fauna is associated with the larger sarcopterygian fishes (see below), and so occurred within the fauna, rather than by transport. Therefore, death by attrition is considered unlikely for the fish of the Canowindra fauna.

In the second scenario, the Canowindra fauna would result from a mass kill of fish in water. Causes of this type of mortality include volcanic activity, influx of toxins, algal blooms, change in water temperature, etc. (reviewed by Zinmeister [1998]). However, this type of death in the water column is believed to result in some degree of decay, disarticulation, transport of skeletal elements, non-life orientations of fish and a thicker layer of fish, none of which is observed in the Canowindra fauna. These are described in more detail below.

Fish dying in water can either float, sink to the substrate or sink to the substrate and be subsequently refloated. Schäfer (1972) noted that under similar water conditions, some fish will float due to gases created by decay, while others will decay entirely at the sediment surface. Schäfer (1972) related this to the size of the body cavity relative to the mass of the fish, and the amount of food present in the stomach upon death. Fish with relatively smaller body cavities result in smaller quantities of gas produced in decay, making the fish less likely to float after death. It is difficult to determine variables like these in fossil fishes, and it is assumed here that the dominant factor in determining whether fish float or sink is water temperature, and the effect water temperature has on rates of decay and production of body gases.

If these temperatures were higher (above 16°C; Elder & Smith, 1988), decay would be greater, and gases produced would tend to cause the fish to float. Decay and water movement would result in skeletal material becoming disarticulated and spread across a wide area (Schäfer, 1972; Elder & Smith, 1988). This water movement need not be strong. Decay and disarticulation were observed for the antiarch *Pterichthyodes* (Achanarras

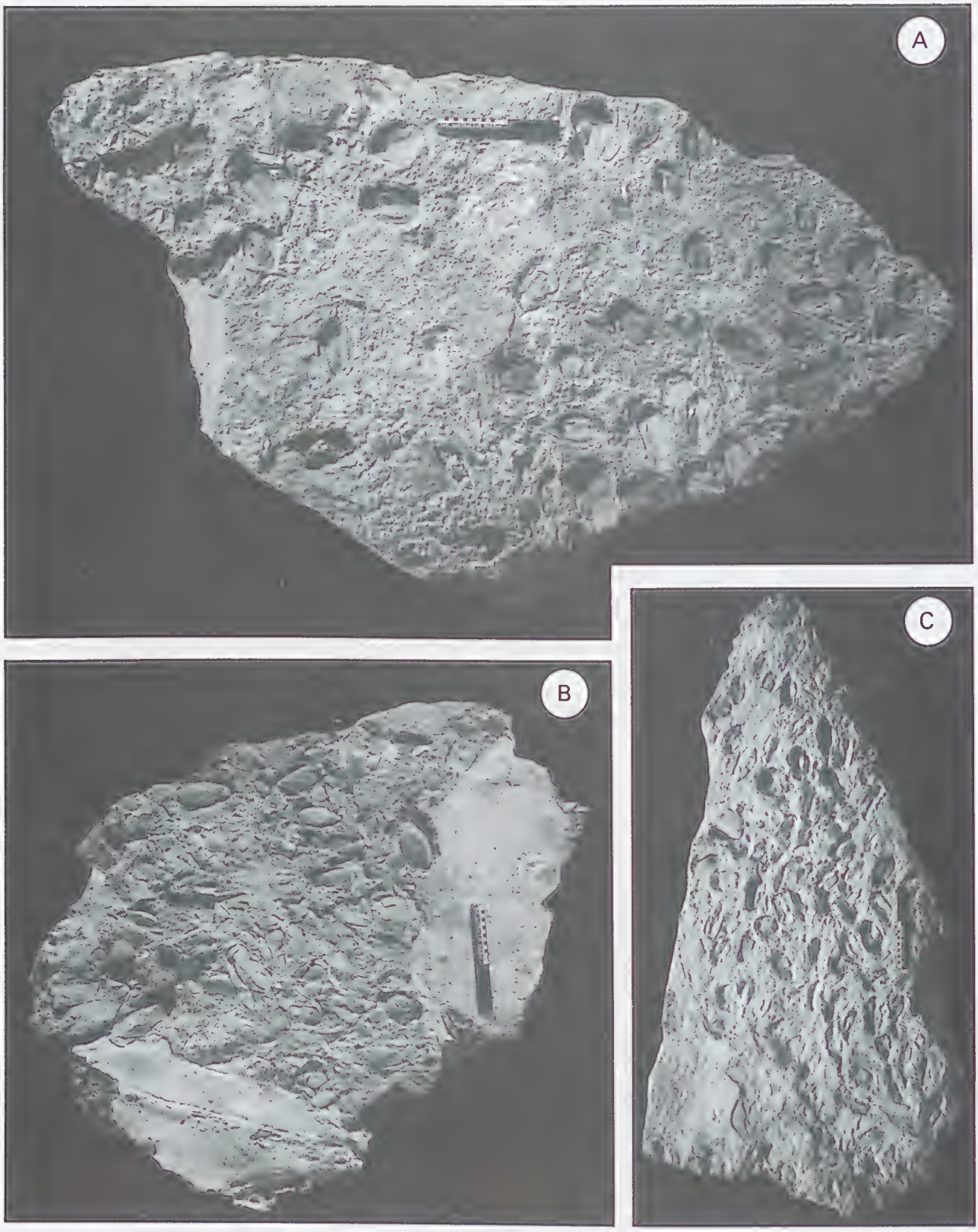

Figure 19. A–C, rock slabs showing dorsal or upper layer of Canowindra fauna, and distribution of fishes on each slab. Fishes are preserved as external moulds with occasional internal cast. The majority of the fishes belong to *Remigolepis walkeri* and *Bothriolepis yeungae*. In B, two large *Mandageria fairfaxi* are preserved, along with disarticulated antiarch plates. Scale in centimetres.

fish bed, Scotland), where dorsal head and trunkshield plates were displaced relative to ventral plates due to movement by weak water currents (Trewin, 1986). Trewin & Davidson (1996) described similar preservation for the acanthodians *Climatius* and *Ischnacanthus* from the Tillywhandland fish bed (Lower Old Red Sandstone, Scotland). This is not characteristic of the Canowindra fauna, where the majority of placoderm and sarcopterygians are well preserved and little disarticulated, including scales (e.g., Figs. 3–10, 13A,B,G,E; also Ahlberg & Johanson, 1997; Johanson, 1997a; Johanson & Ahlberg, 1997). Disarticulation of some antiarchs does occur at Canowindra (Figs. 13C,D,F,G, 14, 15), but this is usually associated with the presence of the larger sarcopterygians (Fig. 19B), as discussed further below. Thus, the Canowindra fauna does not appear to be the result of a mass mortality of fish in warmer waters.

Alternatively, Elder & Smith (1988) noted that in colder water (15°C or lower), fish will sink to the bottom and generally lie intact for an extended period of time, especially if cold or anaerobic conditions preclude the presence of scavengers. Fish will thus be well preserved (as is the Canowindra fauna), particularly if burial is rapid. However, it is assumed that upon dying, fish lose the ability to maintain life orientation as they sink. Counts of individual Canowindra *Bothriolepis* and *Remigolepis* in life (dorsal surface visible, e.g., Fig. 3) *vs* non-life orientation (side or ventral surfaces visible) were made on three randomly selected rock slabs (n = 196 antiarchs). The majority (177 or 91%) of individuals are in life orientation, while 11 are facing down and 8 are on their side.

This life orientation may suggest that the fish from Canowindra did not sink for any substantial distance after death, and so did not die in the water column. But again, the dorsal or life orientation of the majority of the antiarchs may be due to their morphology, with flat ventral and rounded dorsal head and trunkshield surfaces. Antiarchs are also believed to have lived near the sediment surface, especially *Remigolepis* (Stensiö, 1931; Johanson, 1997a), which may result in a preferred dorsal orientation. This result may therefore be somewhat equivocal, although most sarcopterygians with a fusiform body shape are also found in life orientation in the Canowindra fauna (Thomson, 1973; Ahlberg & Johanson, 1997; Johanson & Ahlberg, 1997).

Thus, it is possible that the fish of the Canowindra fauna died as the result of a mass mortality in colder water, sank to the bottom and were well preserved. However, it would be expected that these sinking fish would land on top of one another to some degree, and form a thicker layer on the substrate. Again, this is not observed in the Canowindra fauna, where fish predominantly lie side by side along the bedding plane (e.g., Fig. 19).

The overwhelming absence of disarticulation, decomposition, and the dominant preservation of individuals in life orientation side by side in a single layer along the bedding plane suggest the fish of the Canowindra fauna did not die and decompose in water, nor were individuals transported or collected by moving water. This is consistent with the hypothesis that the Canowindra fauna died in place, with the crowding of the fish occurring prior to death rather than afterwards. The most parsimonious explanation for these observations, particularly the crowding before death, is that the fish became trapped in an ephemeral or temporary pool of water which subsequently dried. Thus, the first scenario listed above is the hypothesis that is followed in discussions below.

Some disarticulation of fish is present in the fauna (Fig. 19B), as seen on a rock slab containing two large individuals of the sarcopterygian *Mandageria fairfaxi*. Between these are scattered and disarticulated antiarch plates. Sarcopterygians had the capacity to breathe air through external and internal nostrils (choanae), and would be able to survive longer in a drying pool. The antiarchs lack this ability and would die before the sarcopterygians. As the *M. fairfaxi* individuals moved, they would disturb these antiarchs and disarticulate their plates. Of interest is the observation that several individuals of *M. fairfaxi* have been noted in the Canowindra fauna, but to date, the rock slab just discussed is the only one where disarticulated antiarchs are noticeably present. If the sarcopterygians could survive longer, more disarticulated and overturned antiarchs would be expected as the sarcopterygians moved through the diminished pool of water. However, by the time oxygen is depleted from the pool, conditions would be so harsh (increased temperature, increased toxicity) that the movement of the sarcopterygians would be minimal, perhaps involving only tail movements in an attempt to aerate remaining water.

Lack of postmortem disarticulation and transport also suggest that the burial was gentle, although the fish could also have become trapped to some degree in drying sediment. Lack of advanced decomposition suggests this burial happened relatively soon after death, or that some degree of mummification occurred during dry conditions (e.g., Weigelt, 1989). The sarcopterygians are collapsed postcranially, suggesting some postmortem decay and flattening of the softer parts of the body. However, decay does not appear to have continued to the point where developing gases caused the body to explode and rupture (e.g., as in *Scaumenacia curta* from the Escuminac Formation, Canada; Parent & Cloutier, 1996). The head and trunkshields of the antiarchs also show no indication of this, and the scale-covered portions of *Remigolepis* are flattened, but not exploded (Johanson, 1997a). Absence of disarticulation could also indicate lack of scavenging. This also suggests burial occurred relatively soon after death.

Burial by a relatively low energy physical agent may also be indicated by the apparent absence of a strong or distinct orientation of fish on individual rock slabs (e.g., Fig. 19), since this agent would tend to reorient individuals in its direction of movement. Additionally, fish may orient themselves side by side in a drying pool of water prior to death, in order to maximise available space (G.C. Young, pers. comm., also Weigelt, 1989), and so would be aligned, but potentially facing opposite directions along this line. Information regarding this orientation is preserved on the individual rock slabs collected, but it is believed that the initial observation of a more random orientation of

individual fish would be best investigated and tested when the *in situ* counterpart of the collected Canowindra fauna is uncovered and available for study. In this way, the orientation of individuals throughout the fauna can be determined.

The above discussion suggests that the fish of the Canowindra fauna died as the result of a single event, that is, isolation of the fish in an ever decreasing pool of water during drier conditions. In this sense (single event, death of a large number of individuals living at the same time), the term "mass mortality" can be applied. Subsequent burial was rapid, but did not transport or disarticulate the fish. The fauna was not subsequently reworked or redeposited. Further analysis of the environment of burial must await a full sedimentological analysis of the rock above and below the fauna, including sedimentological structures. Additional comment on the environment in which the Canowindra fishes lived is deferred until the environment of burial is established. Marine invertebrates have not been discovered in the Canowindra fauna, but taxa like *Bothriolepis* lived in both definite marine (Gogo Formation, Western Australia, e.g., Long, 1995) and freshwater (Catskill Formation, USA, Daeschler *et al.*, 1994) environments. Some recent workers have suggested that many Devonian environments traditionally thought to have fluvial are in fact marine, but evidence based on strontium ratios (Schmidz *et al.*, 1991) of skeletal elements collected from these environments has been equivocal (reviewed by Janvier, 1996). Therefore, care must be taken in the interpretation of the Canowindra environment, based on a future full sedimentological analysis.

Faunal characteristics

A large number of fish have been collected from Canowindra (n = 3033), a sample which represents the original Devonian community. Certain fishes known from other Australian Upper Devonian deposits are absent from Canowindra (phyllolepids, acanthodians, porolepiform sarcopterygians; see Young [1993] for review of these faunas). It is possible that these missing fish groups were present, but not yet collected. For example, these could have been separated from the other Canowindra fishes in distinct pools. This could occur as fish school in different parts of the original habitat, becoming isolated in these areas as the habitat shrinks.

However, the Canowindra fauna shows a greater diversity than fish assemblages described, for example, by Trewin (1986), Wilson (1996) and Trewin & Davidson (1996), the second being dominated by paracanthopterygian fishes and the first and third by acanthodians. Therefore, a reasonable representation of the original Canowindra fish community may have already been collected. It is important to be aware that fossil deposits will always be biased relative to the living assemblage. For example, Smith *et al.* (1988) compared Recent to Early Cainozoic fish faunas and found that floodplain deposits of the latter age preserve only 10–20% of the fish species expected (also G.C. Young, pers. comm.), due to biological and physical destruction of smaller, more delicate fish. Predation certainly could have affected the fish preserved in the Canowindra fauna, but this is believed to have predominantly affected smaller antiarchs (see below), rather than other taxa. Unfortunately, coprolites (perhaps preserving missing fish taxa, e.g., acanthodian fin spines or scales) have not been observed at Canowindra. It is always difficult to evaluate negative evidence (i.e., absence of taxa), so until additional collecting indicates the presence of other types of fishes, the Canowindra assemblage will be considered indicative of the original community, particularly with regards to *Bothriolepis* and *Remigolepis*, whose population profiles at Canowindra are discussed below.

The most abundant fishes, in counts of all 195 rock slabs examined as of 1997, are the antiarchs *Bothriolepis yeungae* (n = 1379 individuals) and *Remigolepis walkeri* (n = 1555). Less common are the euarthrodire *Groenlandaspis* (n = 48) and the sarcopterygians. The number of sarcopterygians in the fauna is low (n = 51 individuals), but they are relatively taxonomically diverse (see pp. 315–316), compared to the antiarchs.

The non-dipnoan sarcopterygians have strongly developed jaws and dentitions, suggesting they were the predators in the fauna, preying predominantly on the placoderms. Caudal fin morphology suggests the sarcopterygians were unsteady rather than steady swimmers (Webb, 1982; Johanson & Ahlberg, 1997; Ahlberg & Johanson, 1997). As unsteady swimmers, these sarcopterygians waited, accelerating and attacking prey as it passed. The caudal fins were also small relative to overall length, and would not have generated a strong accelerating thrust. In contrast, steady swimmers include fishes like the tuna, which swim constantly in search of prey. It may seem unusual that all predators in the Canowindra fauna were unsteady swimmers, but this appears characteristic of many Devonian sarcopterygians (Belles-Illes, 1992).

In contrast, both *Bothriolepis* and *Remigolepis* possess ventral mouths with small, weak lower jaws (Stensiö, 1931, 1948; Johanson, 1997a), suggesting that these fishes were bottom feeders, taking small particles from the sediment surface, or perhaps ingesting and processing the sediment itself for food (Denison, 1941; Weems *et al.*, 1981). However, Johanson (1997a) noted that *Bothriolepis* and *Remigolepis* show differences in jaw structure and inferred musculature as well as in pectoral and more posterior fin morphology, suggesting differences in swimming ability and feeding. *Bothriolepis* is thought to be a more able and manoeuvrable swimmer based on its relatively longer tail and pectoral fins, with the capacity to extend and use its pectoral fins to generate lift and potentially feed within the water column. *Remigolepis* was thought to have been a poorer swimmer with shorter caudal and pectoral fins relative to length (with a reduced capacity for generating lift), and was likely restricted to the bottom. The pectoral fins could also be adducted or swung away from the body in both *Bothriolepis* and *Remigolepis*, perhaps to discourage predation through some type of threat display.

Population characteristics

Size-frequency distributions for *Remigolepis walkeri* and *Bothriolepis yeungae* (Fig. 20) indicate that the Canowindra fauna preserves fewer small individuals, particularly of *Remigolepis*. These size-frequency distributions are based on length (head + trunkshield) measurements taken from specimens on all available (i.e., prepared and latexed) rock slabs, for a total of 343 individuals (n = 233 for *Bothriolepis yeungae* and n = 110 for *Remigolepis walkeri*). This total includes length measurements of the smaller specimens noted above to be too difficult to adequately prepare for individual plate measurements for PCA (Fig. 6). The measurements included a smaller proportion of *Remigolepis* specimens relative to *Bothriolepis*, due to its relatively lower proportion on the slabs prepared, latexed and available for measurement in this analysis (as opposed to counts of individuals from all collected [but often unprepared] rock slabs). The slabs prepared and suitable for measurement were chosen randomly as work on the fauna progressed over the previous three to four years, and thus the specimens measured represent a random sample of both antiarchs.

The size-frequency distributions for both antiarchs are skewed (Fig. 20), *Remigolepis walkeri* towards larger individuals (g1 = –0.36615; kurtosis g2 = 0.68463), and *Bothriolepis yeungae* towards smaller individuals (g1 = 0.42355; kurtosis g2 = 0.55012). Size acts as a proxy for age of the individual in these histograms. Ages of fish can often be determined from skeletal elements such as otoliths and scales (Wootton, 1990), but otoliths are not preserved in the natural moulds present in the Canowindra fauna. Scales are not preserved for *B. yeungae*, while the concentric ridges or circuli needed to determine age are not preserved on the scales of *R. walkeri* (Johanson, 1997a: fig. 18). Growth patterns may be represented on the internal trunkshield of *R. walkeri* (see below), but it would be very difficult to use these to assign absolute ages to these individuals, since these do not necessarily represent yearly growth increments.

Wilson (1984, 1996) commented on the type size-frequency distribution or profile expected in a mass or catastrophic mortality of fish, the effect of which is to sample a living population in a short period of time (Wilson, 1984). Thus, the mass mortality profile would include distinct year-classes or cohorts (fish born at the same time [Wootton, 1990]), represented by multiple peaks in the size-frequency distribution (also Sheldon, 1965; Cummins *et al.*, 1986). Peaks in the size-frequency distribution should also be more distinct for younger individuals, since growth slows in older fish and these peaks become less distinct (Wilson, 1984).

The profiles of *Bothriolepis* and *Remigolepis* possibly show these presumed age classes (Fig. 20, indicated by the arrows), although these are certainly less distinct than in some living fish populations (e.g., Wootton, 1990). However, the size-frequency distributions of *Bothriolepis* and *Remigolepis* do not show distinct peaks for smaller or younger individuals, and in fact,

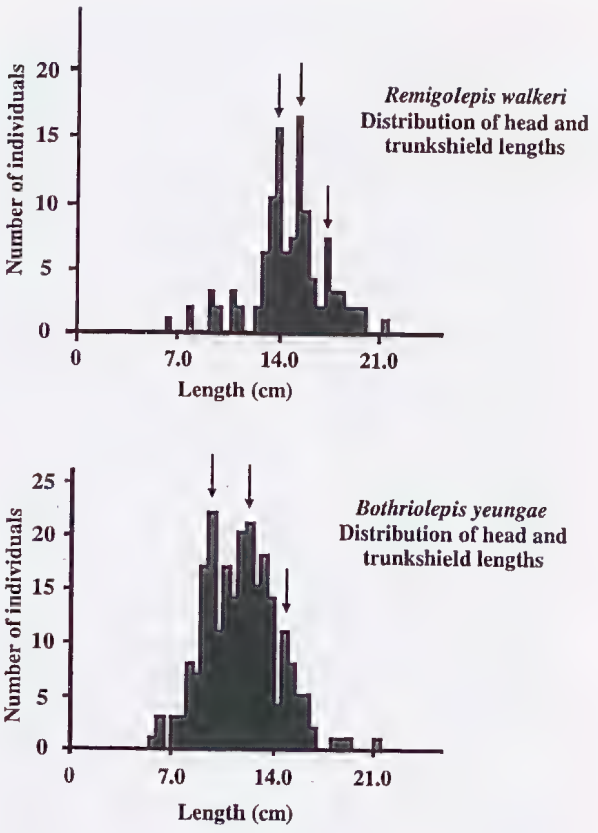

Figure 20. Size-frequency distributions of *Remigolepis walkeri* and *Bothriolepis yeungae*.

specimens of length 5–10 cm make only up 27% of the measured sample of *Bothriolepis yeungae*, while smaller specimens are very rare in the profile of *Remigolepis walkeri* (only 0.06% of the sample). Individuals under 7 cm appear to be rare for both taxa (Fig. 20), and very small juvenile specimens (e.g., similar in size to *Bothriolepis askinae* from the Aztec Siltstone, Antarctica [Young, 1988]) are missing from both population profiles.

The absence of smaller individuals in size-frequency distributions has been reviewed by Cummins *et al.* (1986) and Olszewski & West (1997), including both physical and biological factors. Smith *et al.* (1988) suggest predation by larger fishes on smaller fishes trapped in temporary ponds commonly biases the composition of fish assemblages from Cainozoic floodplain deposits. Predation by the sarcopterygians in the Canowindra fauna could certainly have been important in removing smaller individuals from the fauna. It is assumed that larger antiarchs in the Canowindra fauna would more readily avoid predation. Cummins *et al.* (1986) focus more on bias caused by physical factors such as breakage, dissolution, and abrasion, which can be linked to active transport or movement of the individuals. This can also remove smaller individuals entirely, but it is believed that the Canowindra fauna was little affected by these types of physical processes, as discussed in previous sections.

Another reason why smaller individuals could appear absent from a fauna is sampling bias. Smaller specimens may be overlooked during collection, however, the Canowindra fauna was removed *en masse* by a heavy earth mover, rather than by individual collectors. Smaller specimens can be more difficult to recognise on a crowded rock slab, but this bias is not believed to be large. Additionally, one rock slab preserves smaller individuals of *Bothriolepis yeungae* (but only three smaller fish of *Remigolepis walkeri*, one less than 10 cm), perhaps representing a pool separated from the main Canowindra fauna. If additional rocks from such areas were available for collection, more small fish might be recorded. However, this suggestion remains speculative until more of the fish layer is collected and the presence of these separate pools established. Overall, bias during collection is assumed to be negligible.

Although predation could be a dominant factor in removal of smaller individuals from the Canowindra fauna, the near complete absence of smaller specimens of *Remigolepis* needs to be considered. One possibility may be relatively higher growth rates in *Remigolepis*. *Bothriolepis* and *Remigolepis* plates grow by addition to the outer margins (Stensiö, 1948; Graham-Smith, 1978). On the internal surface of *Remigolepis* plates, concentric lines are visible, separating bands of uneven width (Johanson, 1997a: fig. 15a,b), with wider increments indicating increased growth and narrower indicating reduced growth. These bands can also be observed on East Greenland species of *Remigolepis* (e.g., Stensiö, 1931: pls 7.3, 9.2, 13.1) and less certainly on species from North China (Pan *et al.*, 1987: pl. 16.A1, 18.3, 8.4). Interestingly, on the East Greenland plates, the bands are more equal in size, being wider on some plates (Stensiö, 1931: pl. 7.3) and narrower on others (Stensiö, 1931: pls 9.2, 13.1).

Spacing between growth lines on scales and otoliths of fish is linked to environmental conditions (e.g., Wootton, 1990), whether favourable (wider) or not (narrower). However, the wider bands on trunkshield plates of *Remigolepis walkeri* from Canowindra may be linked to rapid spurts of growth rather than changing environmental conditions as these increments are not observed on plates of *Bothriolepis yeungae* (e.g., Figs. 14–16). The growth spurts may indicate that *Remigolepis* increased rapidly rather than gradually in size. This comparison would be stronger if *B. yeungae* possessed evenly spaced bands on the internal surface of the plates, indicating continuous or more gradual growth. Conversely, gradual growth in if *B. yeungae* may be indicated by the absence of growth lines, if these themselves indicate some type of change or alteration of growth rates.

Another factor to be considered is timing of reproduction. Reproduction in fishes is widely variable among living species and is influenced by environmental factors, food availability for parent and offspring, and presence of predators (Wootton, 1990: 161). The near absence of smaller individuals of *Remigolepis* might suggest differences in timing of reproduction relative to *Bothriolepis*. This might be expected, as these antiarchs numerically dominate the fauna; having different time spawning times would lessen pressure on resources.

Alternatively, the composition of the Canowindra fauna suggests that the mass mortality event resulting in its demise could have occurred during a non-reproductive period for both *Bothriolepis* and *Remigolepis*. Fishes of the same species tend to aggregate when spawning, which was clearly the case in the fauna studied by Wilson (1996), where one species of paracanthopterygian fish dominated the fauna (1700 specimens) to the near exclusion of the other two present (69 osmerids and 2 osteoglossids). Wilson (1996) described the diversity in this fauna as being low, and considered that this might be due to an aggregation of spawning species in a pool of shallow water during a high-water event. The Canowindra fauna differs from this in having a higher taxonomic diversity, and two numerically dominant species, *Bothriolepis* and *Remigolepis*, rather than just one. Even if the antiarchs offset their times of reproduction, as discussed above, it seems unusual that two genera would be present in such large numbers, which would result in increased pressure on various resources and reduce potential success of the reproducing species. This is consistent with the suggestion that lack of juveniles from the Canowindra fauna was due to the mass mortality event occurring during a non-reproductive period. Wilson (1996) was further able to suggest that the fishes in the Joffre Bridge fauna aggregated to spawn because he was able to recognise breeding tubercles (on the males). No such structures have been observed at Canowindra, and further, it is presently impossible to distinguish males from females in the fauna.

Conclusions

The Canowindra fauna, representing the remains of a single Upper Devonian palaeocommunity, is believed to have been trapped in an isolated and ephemeral pool of water that shrank over a restricted period of time during dry conditions. Absence of smaller (younger) individuals of *Bothriolepis yeungae* and *Remigolepis walkeri* appears due to the timing of the mass mortality relative to timing of reproduction of these antiarchs. The smallest specimens would be fish spawned in a previous reproductive season, however, predation on smaller individuals (e.g., Smith *et al.*, 1988) could also have occurred while the temporary pool was drying, removing many of these from the fauna. The absence of small specimens of *Remigolepis* relative to *Bothriolepis* is more difficult to explain, and may be due to differences in growth rates. Reaching large adult size may have had an ecological advantage (in both feeding and avoiding predation) for *Remigolepis*. The term "mass mortality" is applied to the Canowindra fauna, with death occurring over a restricted (but not instantaneous) period of time, affecting individuals living together during this time. Absence of smaller individuals of *Bothriolepis* and *Remigolepis* at Canowindra indicates that population profiles produced by a mass mortality can be affected by biological factors occurring before death, as well as taphonomic factors after death (e.g., Cummins *et al.*, 1986; Smith *et al.*, 1988) and should be interpreted with care.

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Appendix

Model I regression for *Bothriolepis yeungae*. Independent variable is head plus trunkshield length; dependent variables are as below. All variables log transformed to standardise variances. W, width; L, length. Null hypothesis Ho: b = 1; df = 77–2 = 75; t-test: t = b–1/standard error; $t_{[0.05, 75]}$ = 1.665 (approximately).

dependent	a (constant)	b (slope)	standard	t variable	error
W PMD	-0.132664	0.844759	0.09334	1.662 *	accept Ho
L PMD	-0.245285	0.888829	0.760	1.4627 *	accept
W AMD	0.039971	0.751069	0.0825	3.0173 **	reject
L AMD	-0.427343	0.981729	0.05428	0.3371 *	accept
W NU	-0.123761	0.70291	0.12021	2.47166 **	reject
L NU	-0.413476	0.77724	0.0838	2.658 ***	reject
W PP	-0.216405	0.561688	0.08238	5.3237 ***	reject
L PP	-0.73940	0.772064	0.0985	2.31401 *	reject
W ORBFEN	0.151456	0.4904343	0.0948	5.375 ***	reject
L ORBFEN	-0.455043	0.651	0.0948	3.68 ***	reject
LORBM PM	0.455615	0.240687	0.1599	4.7867 ***	reject
L ROSTM PM	-0.2350	0.7179	0.1162	2.4276 **	reject
LPM	-0.9458	1.06105	0.0763	0.8 *	accept

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Neogene to Recent Species of *Krithe* (Crustacea: Ostracoda) from the Tasman Sea and off Southern Australia with Description of Five New Species

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ABSTRACT. The ostracod genus *Krithe* is reported from four grab, two box-core, 62 coretop samples, and Neogene to Quaternary DSDP cores from the abyssal and bathyal regions of the Tasman Sea and off southern Australia. Species identification followed the taxonomic system proposed by Coles *et al.* (1994), in which the anterodorsal radial pore canals are of fundamental importance. A total of 19 species are recognised, five species are described as new: *K. comma, K. dilata, K. pseudocomma, K. prolata*, and *K. triangularis*. Fifteen species are referred to previously described species, and the remaining rare species are left in open nomenclature. Although no living specimens have been recovered, shells of all species have been found in modern sediments and are, therefore, considered to be extant. Overall, the stratigraphic distribution of the species demonstrates an increase in diversity from 3 to 19 species since the Early Miocene, with no extinction. The bathymetric range of most species is wide, though in certain species there are significant differences between the two study regions, such as on the Australian Continental Slope, the relatively much deeper occurrences of *K. triangularis* and *K. marialuisae*, and the absence of *K. dolichodeira* a species found commonly elsewhere. An explanation for such differences is most likely to relate to nutrient, substrate, and oceanographic differences between the two regions.

AYRESS, MICHAEL, TIMOTHY BARROWS, VICKI PASSLOW & ROBIN WHATLEY, 1999. Neogene to Recent species of *Krithe* (Crustacea: Ostracoda) from the Tasman Sea and off southern Australia with description of five new species. *Records of the Australian Museum* 51(1): 1–22.

The benthonic ostracod crustacean genus *Krithe* (Krithidae, Cytheracea, Podocopida) is abundant and widespread in the marine environment, absent only in shallow tropical waters. Despite its wide distribution, it is poorly documented in the Southwest Pacific. Perhaps the most notable study of species from this region is still the pioneering cruise report of the H.M.S. Challenger by Brady (1880). Subsequent studies have avoided identifying *Krithe* to species level, mainly because of the difficulty in classifying taxa with smooth external surfaces which offers few diagnostic characters, and additionally, internal soft-parts are rarely present for study.

Comprehensive studies of *Krithe* are limited mainly to the North Atlantic. The first of these (Peypouquet, 1975, 1977, 1979), reported considerable intraspecific variation, especially in the anterior vestibulum and carapace size. It was proposed that the anterior vestibulum size of different *Krithe* species is inversely proportional to the dissolved oxygen concentration at the sediment-water interface. That large and small vestibule types are often found in the same sample is dismissed by proponents of the hypothesis as inappropriate sampling: carapaces are an instantaneous record of environmental conditions, and that any one sample may include a number of seasonal morphotypes (Carbonel *et al.*, 1997). In recent years, the earlier claims have been challenged (Whatley & Zhao, 1993; van Harten, 1995, 1996) and the taxonomy has been extensively revised often resulting in further subdivision of previously designated species (Coles *et al.*, 1994). In our view, this alternative, more conservative concept of *Krithe* sets limits to intraspecific variation more consistent with that usually observed in species of other podocopid ostracod genera. Such methods have also been employed in other independent, contemporary studies (e.g., Abate *et al.*, 1993).

Biological data of *Krithe* is lacking, though significant observations on a living species, *Krithe praetexta praetexta*, from the Gullmar Fjord, Sweden, has been made in recent years (McKenzie *et al.*, 1989; Majoran & Agrenius, 1995; Agrenius *et al.*, 1997). Elofson (1941) reported an infaunal mode of life for that species, which has been confirmed by observations on living cultures; the species appears to live >1 cm in the sediment (Majoran & Agrenius, 1995). Careful box-core sampling in water depths up to 1,000 m, off California, has also revealed living specimens (rose bengal stained with intact soft-parts) of several species, present usually 1 cm below the sediment surface (Rathburn, 1998, pers. comm.). Given the similarity in carapace shape, such an infaunal mode of life might occur in all but perhaps the most rotund species of *Krithe*. Investigations into the hypothesis concerning the anterior vestibule size and oxygen content of the ambient seawater, in living populations, has been inconclusive (McKenzie *et al.*, 1989).

The purpose of the present study is twofold: (*a*) to describe new species of *Krithe* and document the distribution of all species collected during our extensive sampling of deep-sea sediments off New Zealand and southeast Australia. (*b*) To present the results of direct comparison of our Southwest Pacific material with Atlantic specimens of Coles *et al.* (1994), applying the anterodorsal radial pore canal (ADRPC) type system proposed by Coles *et al.* to initially identify the species.

Material and methods. Material for this study was taken from one grab, 68 coretop, and two box-core samples in the Tasman Sea and Continental Slope regions off southern Australia. Many of the cores also provided us with numerous samples of Quaternary age, dated largely by oxygen isotopic study of the cored sequence. In addition, we have included Pliocene and Pleistocene material from Deep Sea Drilling Project (DSDP) sites of the area, information embodied largely in an unpublished thesis completed during an extensive study programme, co-ordinated by one of us (RCW), investigating deep-sea Ostracoda of the Southwest Pacific (Ayress, 1988; Downing, 1985; Smith, 1983). Undocumented Tertiary material from DSDP sites 592–594 was also made available to us courtesy of Dr K. Swanson (University of Canterbury, New Zealand). Specimens from all nannofossil zones of the Neogene are well preserved and are considered in this study. Poor preservation or undocumented internal carapace features, prevented us from including available Palaeogene data. Table 1 lists details of the site localities (Fig. 1). Ostracod specimens were extracted from the sediment by immersing the samples overnight in a weak 3% solution of hydrogen peroxide and subsequently washing them through a 63 micron mesh sieve. Specimens obtained are disarticulated valves and occasional carapaces. No internal soft-part material was found.

All specimens have been deposited in the micro-palaeontological collections of the Geology Department Museum, Australian National University, Canberra. The catalogue numbers are prefixed ANU.

Systematic palaeontology and comments on species distributions

Krithidae Mandelstam in Bubikyan, 1958

Krithe Brady, Crosskey & Robertson, 1874

Type species. *Ilyobates praetexta* Sars, 1866

Discussion. We found invaluable the system of initial identification based on the nature of the anterodorsal radial pore canals (ADRPC types) indicated by Coles *et al.* (1994), and the following species are ordered according to them. Coles *et al.* observed that, of the five radial pore canals (RPC's) in the anterodorsal region, within a species, one particular canal is much longer than the others. The ADRPC types are based on identifying which is the longest canal. Where the 3rd canal (counting away from the dorsal margin) is longest = type 1, the 2nd canal longest = type 2, the 4th canal longest = type 3. See Fig. 2 and Coles *et al.* (1994, text-figure 1) for additional explanation of terminology.

Further subdivision of the categories was proposed where canals are short, missing, or present as a normal pore. Since the width of the fused zone can vary, short ADRPC's may be present as a normal pore close to the inner margin. It follows that in order to recognise natural groupings, normal pore canals (NPC's) should be considered in ADRPC type recognition where they vary intraspecifically from NPC to RPC, or where they can be shown to be homologous with RPC's in other species. For example, in *Krithe reversa*, AD 2 (the canal immediately below the dorsal-most anterodorsal radial pore canal) is considered by Coles *et al.* (1994) to be

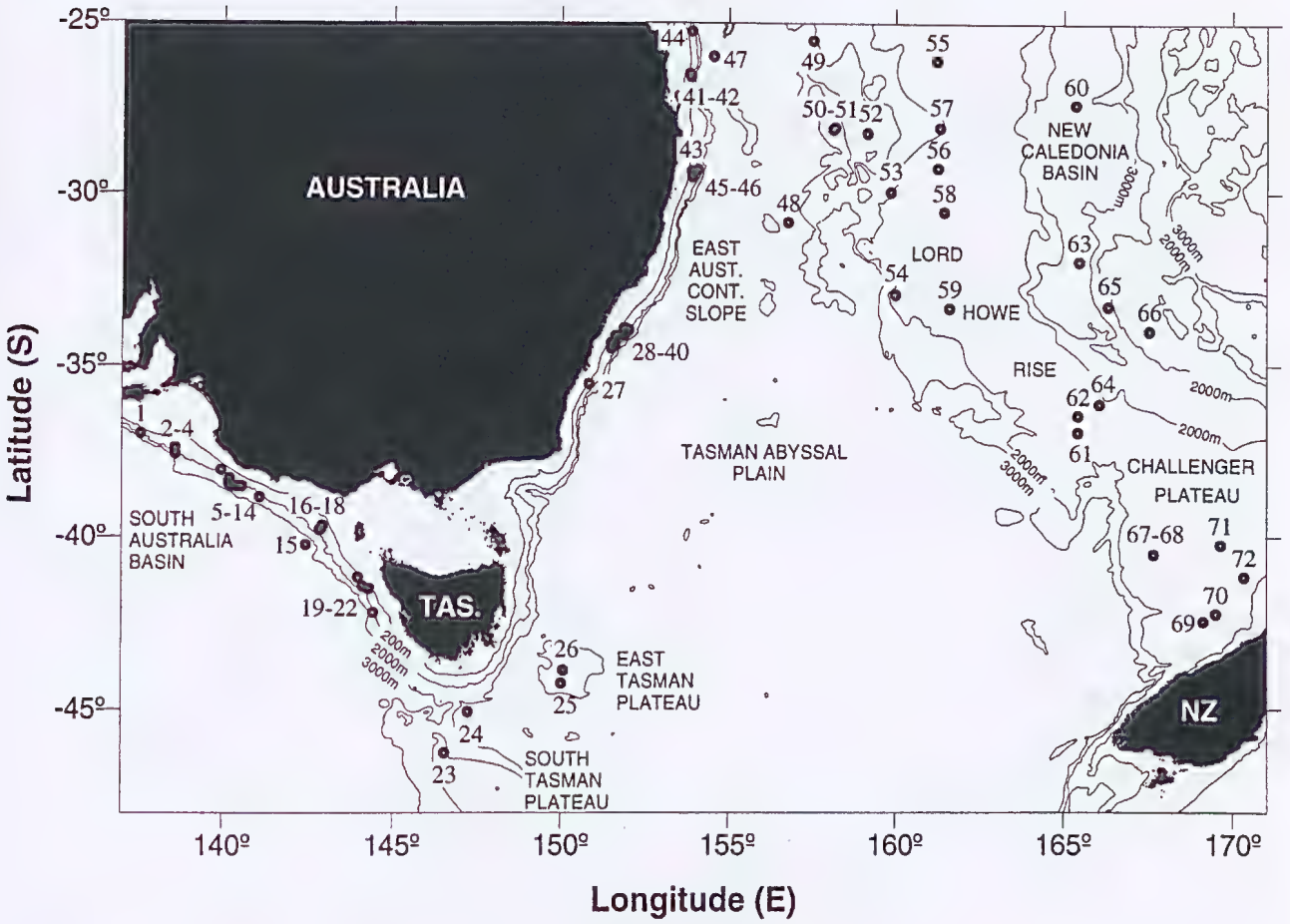

Figure 1. Distribution of sites considered in this report. See Table 1 for map code numbers.

present as a normal pore close to the inner margin. Therefore, the species has ADRPC type 1, rather than type 2, a designation if one was to ignore the normal pore in question.

For this reason, we take great care in illustrating normal pores close to the inner margin. We are less confident that the subdivisional groupings of the ADRPC types can be recognised consistently for the following reasons. (*a*) The width of the fused zone shows significant variability. (*b*) NPC's close to the inner margin can be confused with false RPC's when the shell is very thick, translucent, or strongly inflated, causing oblique viewing of the canal. (*c*) Removal of obscuring sediment retained in the narrow zone between the line of concrescence and the inner margin anterodorsally can be difficult.

The following abbreviations are used: A = adult, LV = left valve, RV = right valve, AD = anterodorsal, RPC = radial pore canal, ADRPC = anterodorsal radial pore canal, NPC = normal pore canal.

Key to Southwest Pacific *Krithe* species

1 Anterodorsal radial pore canal pattern of Type 1 (AD 3 longest) 2

—— Anterodorsal radial pore canal pattern of Type 2 (AD 2 longest) 10

—— Anterodorsal radial pore canal pattern of Type 3 (AD 4 longest) 14

2 Left valve overlaps right valve 3

—— Right valve overlaps left valve ..... *K. reversa*

3 Large (length usually greater than 1 mm) 4

—— Medium to small (length usually less than 1 mm) 5

4 Dorsal margin strongly convex; lateral outline triangular ..... *K. triangularis*

—— Lateral outline subrectangular to subrhomboidal ..... *K. dolichodeira*

5 Anterior vestibulum semicircular in lateral outline 6

—— Anterior vestibulum mushroom or hook-shaped 7

6 Medium sized, moderately well inflated ..... *K. antisawanensis*

—— Small, compressed, usually with long, straight RPC's ..... *K. compressa*

7 Anterior vestibulum narrow and upward curved 8

—— Anterior vestibulum mushroom-shaped 9

8 Anterior vestibulum very narrow; posterodorsal inner lamella wide ..... *K. minima*

—— Anterior RPC's often branching; posterodorsal inner lamella moderately narrow ..... *K. marialuisae*

9 Carapace moderately well inflated, muscle scars small and undivided ..... *K. posticliva*

—— Carapace weakly inflated; muscle scars long, uppermost scar subdivided ..... *Krithe* sp. 1

10 Carapace small, anterior vestibulum small 11

—— Carapace medium to large sized and subrectangular 12

—— Carapace very large and tumid ..... *Krithe* sp. 2

11 Anterior vestibulum bilobed ..... *K. droogeri*

—— Anterior vestibulum at mid-height and elongate ..... *K. perpulchra*

12 Lateral outline subovate; strongly sexually dimorphic; uppermost adductor muscle scar a reclined "F" shape ..... *K. prolata*

—— Outline subrectangular; uppermost adductor muscle scar "U" shaped ..... *K. dilata*

—— Outline subrectangular; uppermost adductor muscle scar subdivided 13

13 Carapace weakly inflated; males strongly sloped dorsally; anterior vestibulum mushroom-shaped ..... *K. comma*

—— Carapace moderately well inflated; sexual dimorphism slight; anterior vestibulum strongly downturned ..... *K. pseudocomma*

14 Carapace very small; anterior RPC's long ..... *K. pernoides sinuosa*

—— Carapace medium to large (length usually less than 1 mm); anterior vestibulum mushroom-shaped ..... *K. morkhoveni morkhoveni*

—— Carapace very large (length usually greater than 1 mm); anterior vestibulum "T" shaped ..... *K. trinidadensis*

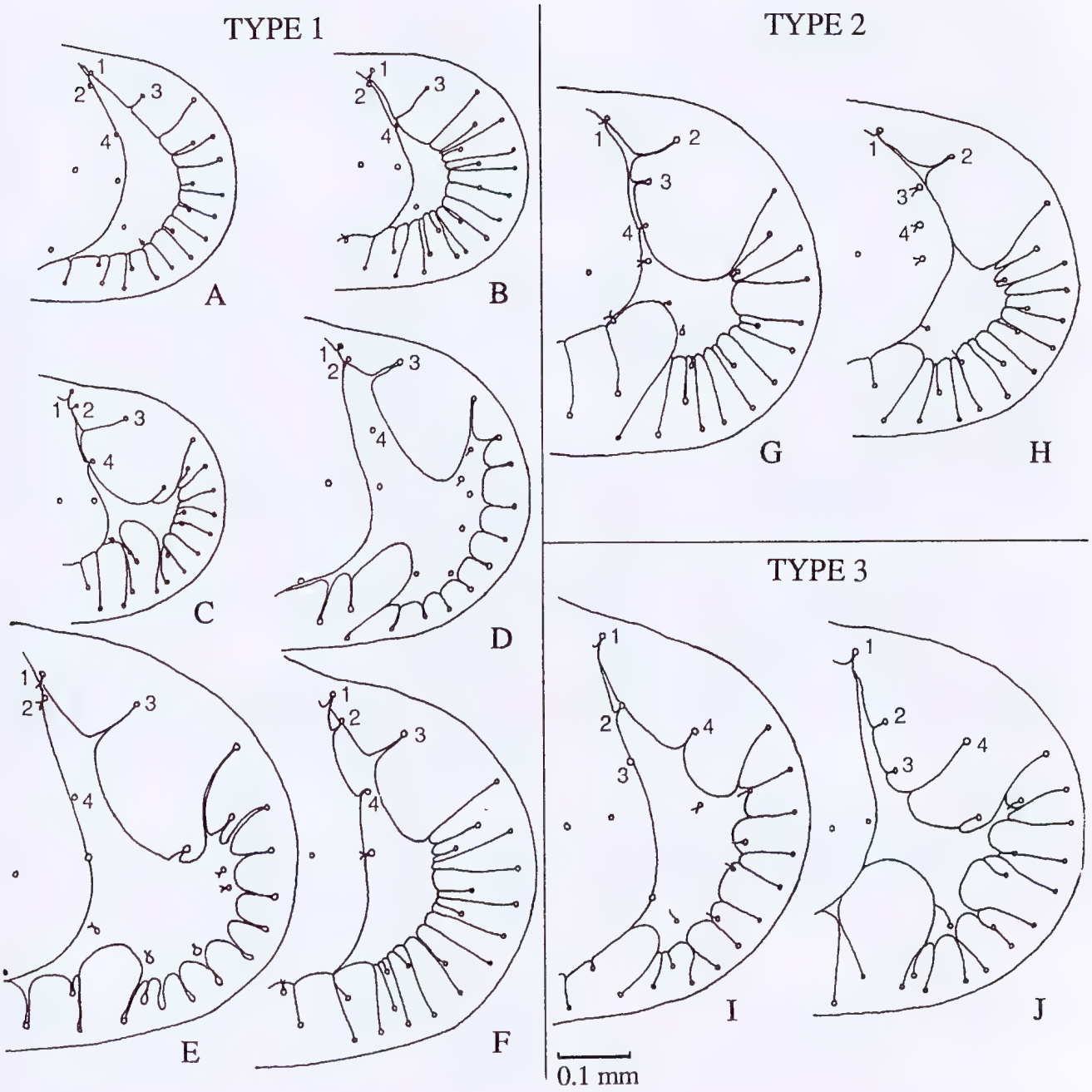

Figure 2. Recognition of the three patterns of anterodorsal radial pore canals (ADRPC types), illustrated by camera lucida drawings of internal valve features. All figures are external views. Anterodorsal radial pore canals or homologous normal pore canals, are numbered 1–4. The three patterns are defined most readily by identifying which of the canals, 1–3 in the anterodorsal region, is the longest. Type 1, canal 3 is longest, shown for example in A, B (*K. compressa*, expanded vestibule form, female RV, ANU 57036, and male RV, ANU 57038, respectively), C (*K. minima*, female RV, ANU 57052), D (*K. dolichodeira* female RV, ANU 57044), E (*K. triangularis*, expanded vestibule form, male LV, ANU 57011, image inverted for ease of comparison), and F (*K. reversa* female LV, ANU 57034, image inverted for ease of comparison). Note that canal 2 is usually a normal pore close to canal 1. It occurs as a short radial pore canal where the fused zone is wide, see C (see also *K. reversa* illustrated by Coles *et al.*, 1994, text-fig. 3D). Canal 4 is always a normal pore. Type 2, canal 2 is longest, and probably homologous to the normal pore close to canal 1 of Type 1 species (the normal pore is absent in Type 2 species); shown for example in G and H (*K. comma*, male RV, ANU 57023, and expanded vestibulum form of male RV, ANU 57026, respectively). Note that where the fused zone is narrow canal 3 is a normal pore, H, and canal 4 is always a normal pore, Type 3, canal 4 is longest, shown for example in I and J (*K. trinidadensis*, expanded vestibulum form, female RV, ANU 57075, and male RV, ANU 57078, respectively). Note that where the fused zone is narrow canals 2 and 3 are normal pores, see I.

ADRPC TYPE 1

Krithe compressa (Seguenza, 1880)

Figs. 2A,B, 3A–D, 8A,B

Ilyobates compressa Seguenza, 1880: 325; pl. 17, figs. 30, 30a.
Krithe aequabilis Ciampo, 1986: 87; pl. 17, figs. 1, 2.–Coles, Whatley & Moguilevsky, 1994: 78; pl. 1, figs. 7–12; text-fig. 3E–K.
Krithe compressa (Seguenza).–Ruggieri, 1991: 60, figs. 5–7.–Abate, Barra, Aiello & Bonaduce, 1993: 354; pl. 3, figs. 1–5; pl. 17, figs. 1, 2.
Krithe sp. 5 Whatley & Zhau, 1993: fig. 3.8.

Remarks. We concur with Abate *et al.* (1993) that *K. compressa* is a senior synonym of *K. aequabilis* Ciampo, 1986. In overall shape it is very similar to *K. marialuisae* Abate *et al.* described from the Plio-Pleistocene of Sicily. However, the anterior vestibule of *K. compressa*, although variable in shape, is usually less upturned than it is in *K. marialuisae*, and the radial pore canals do not bifurcate as they do in the latter species. In addition, *K. compressa* can be distinguished from *K. marialuisae* by its weaker inflation. Both species are common in our material.

The width of the anterior fused zone varies somewhat, and the normal pore close to AD 1 sometimes becomes a short AD 2 (Coles *et al.*, 1994). In species which have ADRPC of type 2 there is no normal pore in this position but instead a long RPC is present. For this reason we suggest that the normal pore is homologous to AD 2 in other species. Therefore, to maintain natural relationships of the ADRPC system, we include the normal pore when counting ADRPC's. Thus, we assign this species to an ADRPC category of type 1B.

Distribution. Occurs widely throughout the study region at water depths from 759 to 3281 m.

Stratigraphical range. Late Miocene (NN 11a) to Recent, based on core records of DSDP sites 208, 284, 592 and 593.

Krithe antisawanensis Ishizaki, 1966

Figs. 3E,F, 8C,D

Krithe antisawanense [sic] Ishizaki, 1966: 137, pl. 18, figs. 17, 24, 25.–Zhau, 1988: 243, pl. 42, figs. 1, 2.–Zhou & Ikeya, 1992: 1111, figs. 9.4, 9.5.

Remarks. This species appears to be identical to *K. reversa* Bold except in having normal overlap (Ishizaki, 1966). Like *K. reversa* there is a normal pore close to AD 1 homologous to AD 2.

Distribution. This is the most widespread species of this study, ranging in depth from 686 to 3403 m.

Stratigraphical range. Middle Miocene (NN 6) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593.

Krithe dolichodeira Bold, 1946

Figs. 2D, 3G,H, 8E,F

For comprehensive pre-1988 synonymy see Coles *et al.* (1994)

Krithe dolichodeira Bold, 1946: 75, pl. 4, figs. 14a,b.–Coles, Whatley & Moguilevsky, 1994: 81; pl. 1, figs. 13–18; text-fig. 3L–Q.
Parakrithe hemideclivata Ruan in Ruan & Hao, 1988: 272, pl. 45, figs. 12–15.
Krithe spatularis Dingle, Lord & Boomer, 1990: 272, figs. 16D–F, 17B, 18E.
Krithe hemideclivata (Ruan).–Whatley & Zhau, 1993: fig. 3.9.

Remarks. The characteristic mushroom shaped anterior vestibulum varies in our material, particularly in the width of the neck and dorsally. In this regard, and also in the lateral outline, our material is very close to an Atlantic species illustrated by Coles *et al.* (1994, text-fig 3AA–DD) as *Krithe* sp. cf. *K. hiwanneensis* (Howe & Law). However, our material is much larger than that species. In size it closely matches those specimens examined by Dingle *et al.* (1990) (named *K. spatularis*) from off South Africa, and also Quaternary specimens cited by Coles *et al.* (1994: 81). This is to be expected given the relatively young age of our material.

Distribution. Recorded in our study region at depths from 686 to 3281 m, only in the eastern and northern parts of the Tasman Sea.

Stratigraphical range. Late Miocene (NN 11b) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593. The species is also known to occur much earlier from the Early Eocene zone NP 10 (Coles *et al.*, 1994).

Krithe marialuisae Abate, Barra, Aiello & Bonaduce, 1993

Figs. 3I,J, 8G,H

Krithe sp. 3 Ciampo, 1980: 17; pl. 4, fig. 4.
Krithe marialuisae Abate, Barra, Aiello & Bonaduce, 1993: 361; pl. 2, figs. 1–5; pl. 6, fig. 5.

Remarks. The Sicilian material described by Abate *et al.* (1993) is somewhat smaller (length of holotype 0.58 mm), but in all other respects our material appears to conform to this species. It is similar to *Krithe sphaenoidea* Ruan (in Ruan & Hao, 1988), from the Okinawa Trough. However, judging from the illustrations given, that species appears to have a more convex ventral margin and straighter anterior RPC's.

Distribution. The species is distributed throughout the study region, ranging in depth from 1066 to 2860 m.

Stratigraphical range. Middle Miocene (NN 7) to Recent, based on core records of DSDP sites 207, 208, 284, 592 and 593.

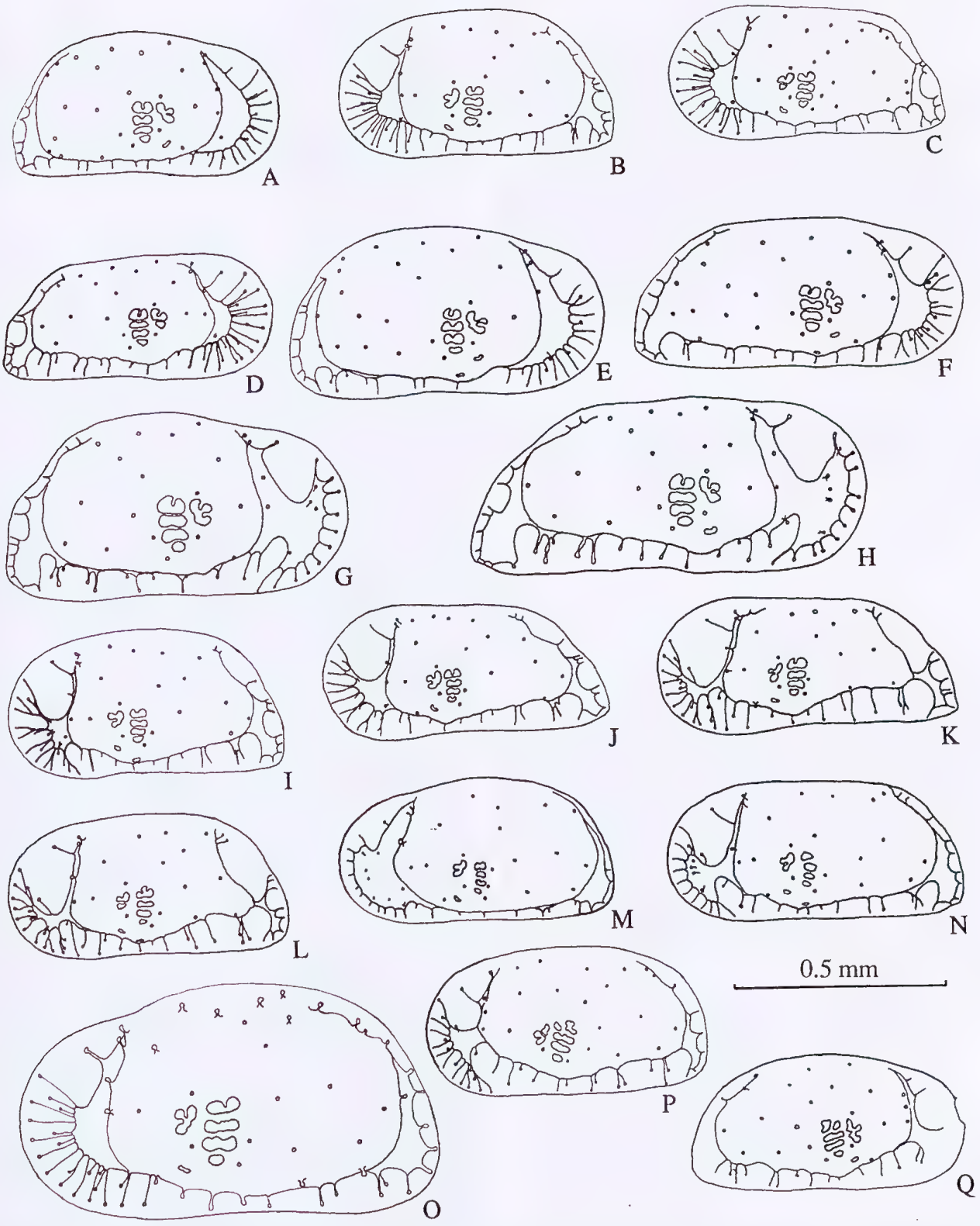

Figure 3. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, *Krithe compressa* Seguenza, A, female right valve (ANU 57036), 71GC44, 100 cm, B, female left valve (ANU 57035), SO-36-61, 157 cm, C, male left valve (ANU 57037), 71GC44, 15 cm, Holocene, D, male right valve (ANU 57038), 71GC44, 15 cm, Holocene; E–F, *Krithe antisawanensis* Ishizaki, E, female right valve (ANU 57040), 67GC03, 274 cm, F, male right valve (ANU 57042), 67GC03, 280 cm; G, H, *Krithe dolichodeira* Bold, G, female right valve (ANU 57044), SO-36-61, 144.5 cm, H, male right valve (ANU 57046), SO-36-61, 157 cm; I, J, *Krithe marialuisae* Abate *et al.*, I, female left valve (ANU 57047), 1/86 6GC3, 125 cm, J, male left valve (ANU 57049), SO-36-61, 144.5 cm; K, L, *Krithe minima* Coles *et al.*, K, male left valve (ANU 57053), SO-36-61, 117 cm, L, female left valve (ANU 57051), SO-36-61, 148.5 cm; M, N, *Krithe posticliva* Hao, M, female left valve (ANU 57055), 71GC44, 15 cm, N, male left valve (ANU 57057), 71GC26, 15 cm; O, *Krithe reversa* Bold, female left valve (ANU 57034), 71GC26, 22 cm; P, Q, *Krithe* sp. 1, P, female? left valve (ANU 57017), 105GC20, coretop, Q, female? right valve (ANU 57018), 105GC20, coretop.

Krithe minima
Coles, Whatley & Moguilevsky, 1994

Figs. 2C, 3K,L, 8I,J

Krithe minima Coles, Whatley & Moguilevsky, 1994: 88; pl. 2, figs. 16–18; pl. 3, figs. 1–5; text-fig. 3EE–JJ.

Remarks. The species is distinct by virtue of its relatively small size, very narrow crescentic anterior vestibule, and wide posterodorsal inner lamella. In our material there are two short anterodorsal radial pore canals (AD 1 and AD 2), AD 2 sometimes being present as a normal pore. Thus, the elongate radial pore is AD 3 indicative of ADRPC Type 1A, and 1B where AD 2 is a normal pore.

Distribution. Found at water depths of 1066 to 3281 m in the Tasman Sea.

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593. The species is very common throughout the Neogene.

Krithe posticliva (Hao in Ruan & Hao, 1988)

Figs. 3M,N, 8K,L

Parakrithella posticliva Hao in Ruan & Hao, 1988: 273, pl. 45, figs. 8–11.–Ruan, 1989: 121, pl. 22, figs. 14, 15.

Remarks. The mushroom-shaped anterior vestibulum of this species is sometimes greatly expanded proximally. *Krithe posticliva* is similar to *Krithe exigua* and *K. marialuisae*, both described from the Plio-Pleistocene of Sicily by Abate *et al.* (1993). However, *K. posticliva* differs from both species in its more truncate posterior margin and is more elongate.

Distribution. The species is rare in our study, found only on the eastern Australian continental slope from 989 to 1989 m.

Stratigraphical range. Late Pliocene (NN 16) to Recent, based on core records of DSDP site 593.

Krithe reversa Bold, 1958

Figs. 2F, 3 O, 8M

For comprehensive pre-1988 synonymy see Coles *et al.* (1994).

Krithe reversa Bold, 1958: 404, pl. 1, figs. 4a–g.–Coles, Whatley & Moguilevsky, 1994: 77; pl. 1, figs. 1–6; text-fig. 3A–D.
Krithe tumida Nohara, Itose & Tabuki, 1988: pl. 2, fig. 1.
Krithe sawanensis Hanai, 1959.–Ruan & Hao, 1988: 269; pl. 40, figs. 21–23; pl. 44, figs. 11–17.–Ruan, 1989: 121, pl. 22, fig. 12.–Whatley & Zhao, 1993: figs. 2, 3.–Zhou & Ikeya, 1992: 1108, fig. 3 (uppermost), fig. 7 (lower), figs. 9.1–9.3, figs. 10.1–10.3.
Krithe sp. 4 Dingle, Lord & Boomer, 1990: 282, figs. 17D, 18F, 22E.

Distribution. This species is not common, but is widely distributed, occurring at almost all sites in our study region. It was found at depths from 850 to 3552 m.

Stratigraphical range. Early Pliocene (NN 13) to Recent, based on core records of DSDP sites 206, 208 and 284. The earliest known record of the species is Middle Miocene zone NN 6 (Coles *et al.*, 1994).

Krithe triangularis n.sp.

Figs. 2E, 4A–H, 8N,O

Krithe sp. 14 Coles, Whatley & Moguilevsky, 1994: text-fig. 6T,U.

Etymology. Latin, triangular. Referring to the triangular lateral outline especially of males of this species.

Type material and dimensions. HOLOTYPE, ANU 57011, male LV, length 1.26 mm, height 0.58 mm. PARATYPES: ANU 57012, male RV, length 1.24 mm, height 0.55 mm, core SO-36-61, interval 37 cm; ANU 57013, female LV, length 1.12 mm, height 0.61 mm, core SO-36-61, interval 157 cm; ANU 57014, female RV, length 1.08 mm, height 0.57 mm, core SO-36-61, interval 157 cm; ANU 57015, female LV, length 1.12 mm, height 0.66 mm, core 71GC026, interval 60 cm. All specimens are of Late Pleistocene age.

Type locality and horizon. Western flank of Lord Howe Rise, present day water depth 1340 m, Sonne core 36-61, interval 69 cm, Late Pleistocene.

Diagnosis. A very large species of *Krithe* with pronounced sexual dimorphism. Males subrectangular to subtriangular in lateral view, with dorsal margin gently convex throughout shell length; females are much shorter and less tapering posteriorly. Inner lamella is narrow posterodorsally, wide posteroventrally with a large posterior vestibulum. The anterior vestibulum is large and mushroom-shaped with variable neck width. ADRPC of type 1B.

Description. Carapace large, strongly sexually dimorphic: in lateral outline males are subtriangular to subrectangular, females rectangular and considerably shorter. Dorsal margin in both sexes is gently convex throughout, except in RV which has a slight concavity at anterior third of length. In males the dorsal margin tapers to an acute posteroventral angle interrupted by a distinct mid-posterior shoulder. In females the posterior is more truncate. Ventral margin usually straight in females, gently to strongly concave in males. Normal overlap. Inner lamella narrow dorsally and mid ventrally, wide elsewhere. Anterior vestibulum is large and mushroom-shaped with variable neck width; dorsal lobe usually more strongly developed than ventral lobe. ARPC's are short to moderately long. ADRPC of type 1B. AD 1 and 2 are closely adjacent. AD 1, 2 and 4 are normal pores, which are situated, when viewing valve in lateral aspect, usually between line of concrescence and inner margin, or rarely just behind inner margin. Posterior vestibulum is deep with wide neck. Muscle scars large, often with very meandering outlines but are not subdivided.

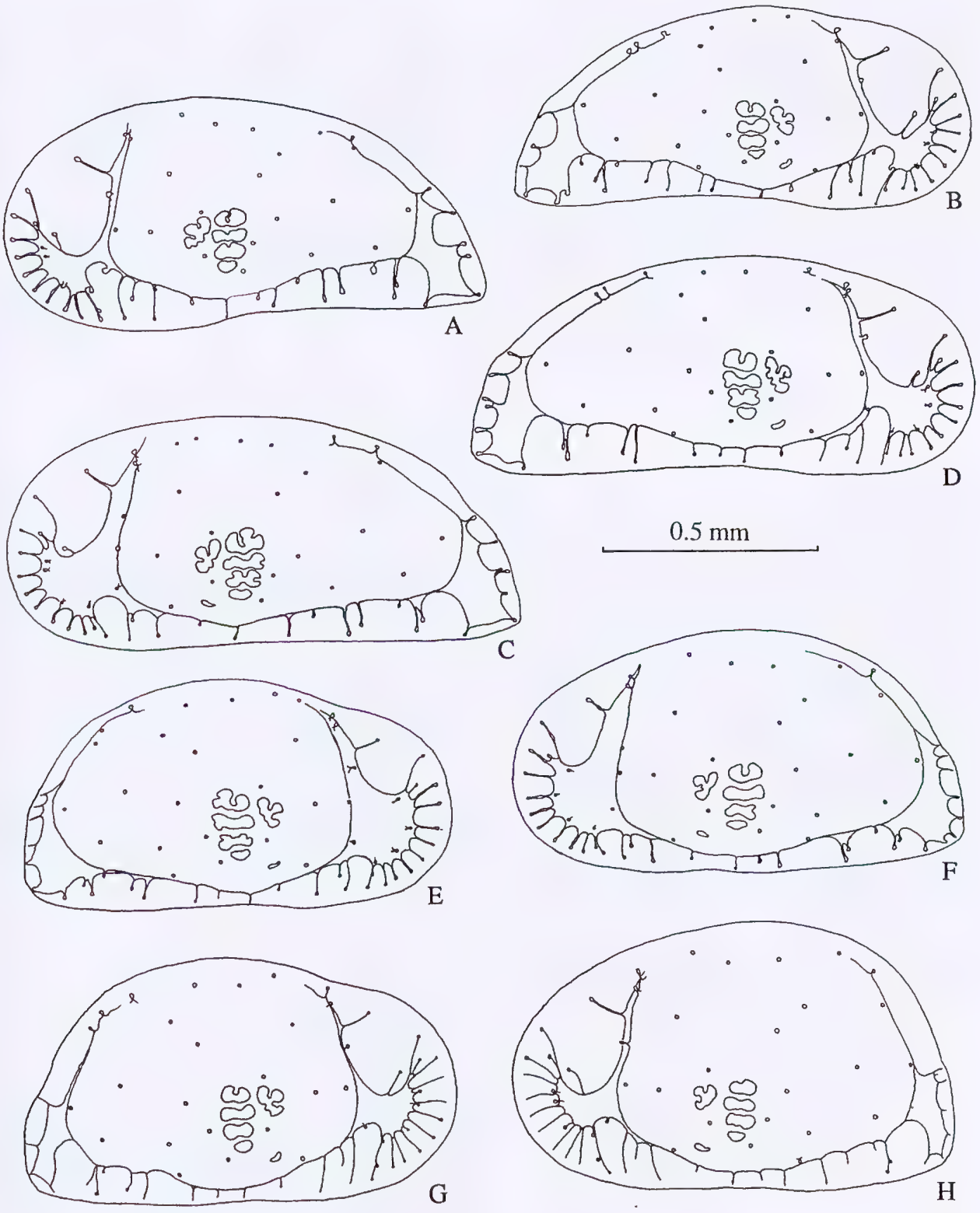

Figure 4. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–H, *Krithe triangularis* n.sp., A, male left valve (P. Smith M.Sc collection, UC Aberystwyth), 208/3/3, late Pliocene, B, male right valve (P. Smith M.Sc collection, UC Aberystwyth), 208/3/3, late Pliocene, C, male left valve (holotype, ANU 57011), SO-36-61, 69 cm, D, male right valve (ANU 57012), SO-36-61, 37 cm, E, female right valve (ANU 57014), SO-36-61, 157 cm, F, female left valve (ANU 57013), SO-36-61, 157 cm, G, female right valve of carapace (ANU 57015), 71GC26, 60 cm, H, female left valve of carapace (ANU 57015), 71GC26, 60 cm.

Remarks. Males of *K. triangularis* show considerable variation in the degree of posterior acumination. Weakly acuminate forms and females can be confused with *K. antisawanensis*. However, *K. triangularis* can be distinguished easily from that species in its mushroom-shaped anterior vestibulum and larger carapace.

Distribution. Widely distributed particularly in the East Tasman Sea, where it occurs at depths from 1125 to 3281 m. The species is somewhat deeper, ranging no shallower than 1818 m, on the Australian Continental Slope (Table 1).

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 207, 208, 284, 592 and 593. The species is very rare in the Late Miocene.

Krithe sp. 1

Figs. 3P,Q, 8P

Description. Carapace very small and weakly inflated. Lateral outline subrectangular; sexes not apparent. Dorsal margin gently convex throughout, except in RV which has a slight concavity at anterior quarter of length. Posterior margin convex dorsally, truncate ventrally with mid-posterior shoulder almost indistinct. Ventral margin is straight. Normal overlap. Inner lamella narrow postero-dorsally moderately wide elsewhere. Anterior vestibulum mushroom-shaped, weakly expanded distally, and with a moderately narrow neck. ARPC's are moderately long. ADRPC of type 1B. AD 2 and 4 are normal pores. Posterior vestibulum narrow. Adductor muscle scars large except for the lowermost scar which is much smaller; the uppermost scar is subdivided into two. Frontal scar trefoil, sometimes subdivided.

Remarks. The species is distinct by virtue of its very small size and weak inflation. It is left in open nomenclature due to the paucity of material.

Distribution. Found only at 355 m on the eastern Australian continental slope. A single specimen has also been found in the Early Pleistocene of DSDP site 284.

ADRPC TYPE 2

Krithe droogeri Keij, 1953

Figs. 5A,B, 8Q

Krithe droogeri Keij, 1953: 159, pl. 1, figs. 6a,b, 7.–Ruan & Hao, 1988: 269, pl. 44, figs. 1, 2.
Krithe sp. cf. *K. droogeri* Keij.–Whatley & Zhao, 1993: 288, fig. 3.14.

Remarks. The species is very distinctive by virtue of its small bilobed anterior vestibulum and branching radial pore canals. There is some variation in lateral outline: the dorsal margin is arched in our specimens, but in the China Sea, specimens illustrated by Ruan & Hao (1988) and Whatley & Zhao (1993) it is straight. Sexual dimorphism may explain these differences. Although we found too few specimens to distinguish the sexes in our material, the convex dorsal margin suggests that they are all female.

Distribution. Found between 1200 and 1989 m on the eastern Australian continental slope.

Stratigraphical range. The species is very rare and found sporadically from the Middle Miocene (NN 6) to Recent. The fossil occurrences are from DSDP cores 206 and 592.

Krithe perpulchra
Abate, Barra, Aiello & Bonaduce, 1993

Figs. 5C–E, 8R

Krithe perpulchra Abate, Barra, Aiello & Bonaduce, 1993: 364; pl. 3, figs. 6–9; pl. 6, fig. 13.

Remarks. Very few specimens of this species were found and of those only females were well preserved. Although Abate *et al.* (1993) illustrate and describe only males, our specimens clearly show the anteriorly tapering anterior vestibulum characteristic of this species.

Distribution. Found at 759 m, 773 m and, probably transported (single poorly preserved male specimen) at 1321 m off eastern Australia.

Stratigraphical range. Late Pleistocene (NN 21) to Recent, based on numerous piston core records from the Australian Continental Slope. The earliest known occurrence of this species is Pliocene Zone M Pl 4 of Sicily (Abate *et al.*, 1993).

Krithe prolata n.sp.

Figs. 5F–I, 8S,T

? *Krithe* sp. Guernet, 1993: 348, pl. 1, fig. 10.

Etymology. Latin, elongated. Referring to the elongate shape of this species.

Type material and dimensions. HOLOTYPE, ANU 57019, male LV, length 1.21 mm, height 0.52 mm. PARATYPES: ANU 57020, male RV, length 1.12 mm, height 0.50 mm, core 67GC03, interval 56 cm; ANU 57021, female LV, length 0.99 mm, height 0.51 mm, core 67GC03, interval 56 cm; ANU 57022, female RV, length 0.96 mm, height 0.47 mm, core 67GC03, interval 7 cm. All specimens are Late Pleistocene in age.

Type locality and horizon. Continental slope off southeastern Australia, present day water depth 1476 m, AGSO core 67GC03, interval 7 cm, Holocene.

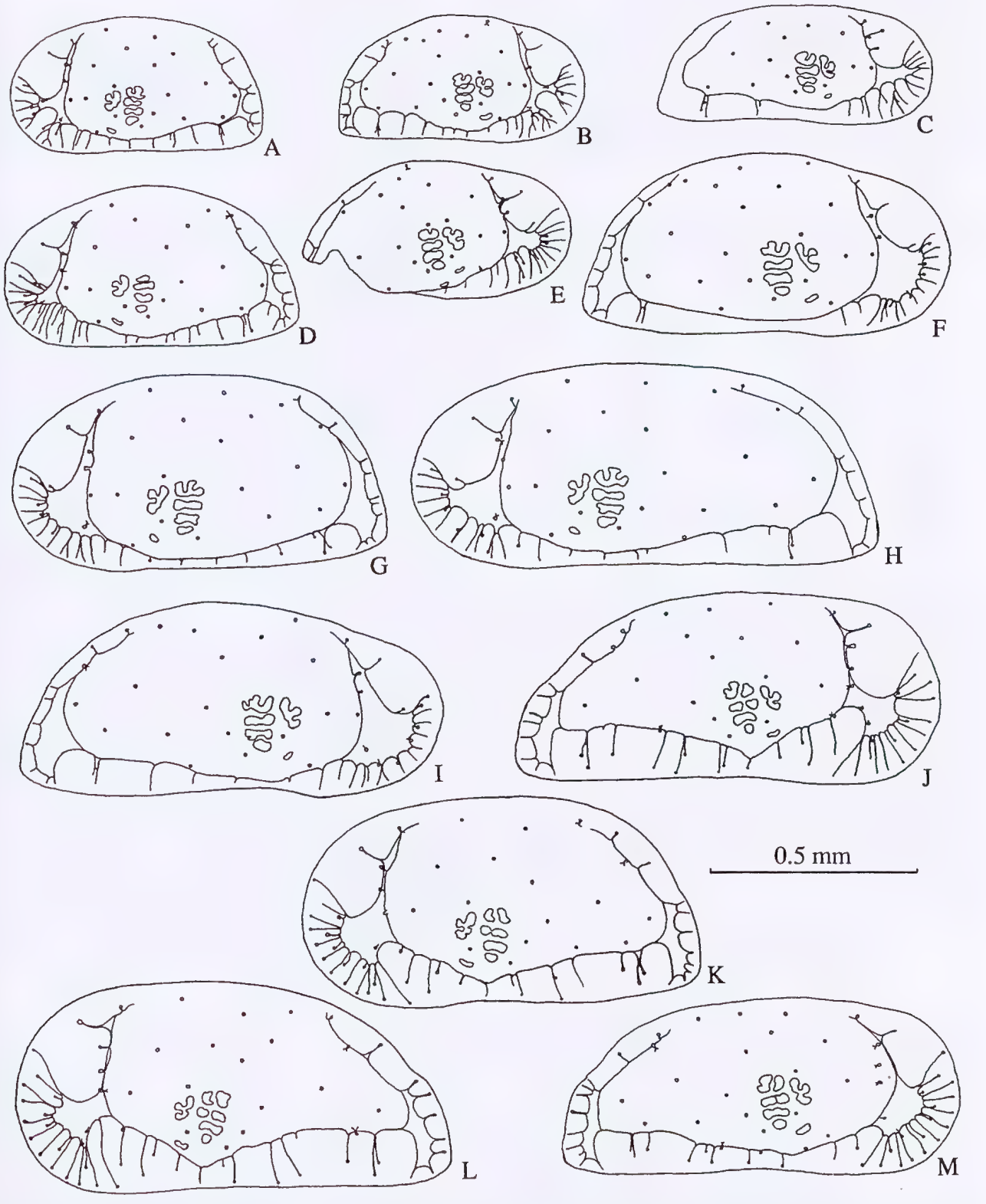

Figure 5. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A, B, *Krithe droogeri* Keij, A, female left valve (ANU 57059), 71GC44, 15 cm, Holocene, B, female right valve (ANU 57060), 71GC44, 15 cm, Holocene; C–E, *Krithe perpulchra* Abate *et al.*, C, male right valve (ANU 57063), 71GC44, 160 cm, D, female left valve (ANU 57061), 5/91 40Pc10A, coretop, E, female right valve (ANU 57062), 5/91 40Pc10A, coretop; F–I, *Krithe prolata* n.sp., F, female right valve (ANU 57022), 67GC03, 7 cm, G, female left valve (ANU 57021), H, male left valve (holotype, ANU 57019), 67GC03, 7 cm, I, male right valve (ANU 57020), 67GC03, 56 cm; J–M, *Krithe comma* n.sp., J, male right valve (holotype, ANU 57023), SO-36-61, 12 cm, K, female left valve (ANU 57025), GR5/4, 6 cm, Holocene, L, male left valve (ANU 57024), SO-36-61, 12 cm, M, female right valve (ANU 57026), GR5/4, 6 cm, Holocene.

Diagnosis. A very large species of *Krithe* with pronounced sexual dimorphism. Males elongate subrectangular in lateral view, females much shorter. In both sexes dorsal margin is weakly convex, almost straight in LV. Posterior margin steeply inclined with shallow indentation. Inner lamella narrow posterodorsally. Anterior vestibulum moderately large and subtriangular. ADRPC of type 2B. Dorsal adductor scar is narrow with an anterior and a medial dorsally directed lobes.

Description. Carapace large, strongly sexually dimorphic: in lateral outline males elongate subrectangular, females subrectangular and considerably shorter. Dorsal margin in both sexes gently convex throughout, except in RV which has a very slight concavity at anterior quarter of length. Anterior margin strongly convex; posterior margin truncate and steeply inclined. Ventral margin straight or weakly concave. Normal valve overlap. Inner lamella narrow dorsally and mid ventrally, moderately wide elsewhere. Anterior vestibulum subtriangular in lateral aspect and weakly upturned distally. ARPC's short to moderately long. ADRPC of type 2B. AD 1 often a short false RPC or a normal pore. AD 2 and 4 are normal pores. Posterior vestibulum moderately deep with wide neck. Muscle scars large, outline of the upper adductor is a reclined "F" shape.

Remarks. The species can be confused with *K. antisawanensis* which differs mainly in its ADRPC type. The shape of the adductor muscle scars also serves to readily distinguish the species. A similarly elongate species from the Miocene of the Exmouth Plateau, Indian Ocean, is illustrated by Guernet (1993, pl. 1, fig. 10) and may be conspecific; internal features were not given.

Distribution. *Krithe prolata* occurs rarely on the eastern Australian continental slope from 1270 to 1989 m.

Stratigraphical range. Late Pleistocene (NN 21) to Recent, based on piston core records from the Australian Continental Slope.

Krithe comma n.sp.

Figs. 2G,H, 5J–M, 8U,V

Etymology. Latin, mark of punctuation. Referring to the lateral outline of this species resembling a comma.

Type material and dimensions. HOLOTYPE, ANU 57023, male RV, length 1.12 mm, height 0.48 mm. PARATYPES: ANU 57024, male LV, length 1.13 mm, height 0.52 mm, core SO-36-61, interval 12 cm; ANU 57025, female LV, length 1.03 mm, height 0.53 mm, core GR 5/4, interval 6–8 cm; ANU 57026, male RV, length 1.05 mm, height 0.45 mm, core GR 5/4, interval 6–8 cm. In age specimens from SO-36-61 are latest Pleistocene; those from GR 5/4 are Holocene.

Type locality and horizon. Western flank of Lord Howe Rise, present day water depth 1340 m, Sonne core 36-61, interval 12–13 cm, latest Pleistocene.

Diagnosis. A very large, compressed species of *Krithe* with strong sexual dimorphism. Males elongate with long posterodorsal slope and deep posterior indentation. Inner lamella wide posterodorsally. Anterior vestibulum rhomboidal and only weakly distally expanded, particularly dorsally. ADRPC of type 2A; AD 3 is a short RPC, AD 4 is a normal pore. Upper two adductor scars are frequently subdivided.

Description. Carapace very large, very weakly inflated, strongly sexually dimorphic. In lateral outline males are subrectangular, females considerably shorter, and more truncate posteriorly. Dorsal margin in both sexes straight and parallel with ventral margin through anterior two thirds of valve length, convex posteriorly tapering to a distinct mid-posterior shoulder. Posteroventral margin truncate with deep indentation. Ventral margin variably straight to gently concave. Normal valve overlap. Inner lamella moderately wide dorsally and ventrally, very wide anteriorly. Anterior vestibulum moderately large, rhomboidal with variable neck width, and only weakly distally expanded particularly dorsally. ARPC's are long. ADRPC of type 2A. AD 1 a short RPC or normal pore, AD 3 a short RPC rarely a normal pore, and AD 4 a normal pore emergent just behind the line of concrescence. Posterior vestibulum moderately narrow. Muscle scars large, the upper two adductors usually subdivided.

Remarks. The species has the unusual ADRPC pattern of type 2A, a pattern unrepresented in Atlantic species. It shares this pattern, and many other internal features, with *K. pseudocomma*. However, *K. comma* is easily distinguished from that species by its much weaker inflation, more produced posterior, and less ventrally expanded vestibulum.

Distribution. A species occurring at relatively shallow depths (702 to 1340 m) only on the Lord Howe Rise.

Stratigraphical range. Middle Miocene (NN 6) to Recent, based on core records of DSDP sites 207, 284, 592 and 593. This species occurs commonly throughout its range, and probably evolved from *K. pseudocomma*.

Krithe dilata n.sp.

Figs. 6A–D, 8W,X

Krithe sp.–Swanson, 1979: 33; fig. 43.
Krithe sp. 1.–Ruan & Hao, 1988: 271; pl. 44, figs. 23–25; pl. 45, figs. 1, 2.

Etymology. Latin, dilate. Referring to the considerable expansion of the anterior vestibulum often displayed in this species.

Type material and dimensions. HOLOTYPE, ANU 57031, female RV, length 1.00 mm, height 0.51 mm. PARATYPES: ANU 57032, female LV, length 0.99 mm, height 0.56 mm, core 71GC044, interval 1.00–1.01 m; ANU 57033, female RV, length 0.92 mm, height 0.49 mm, core 71GC044,

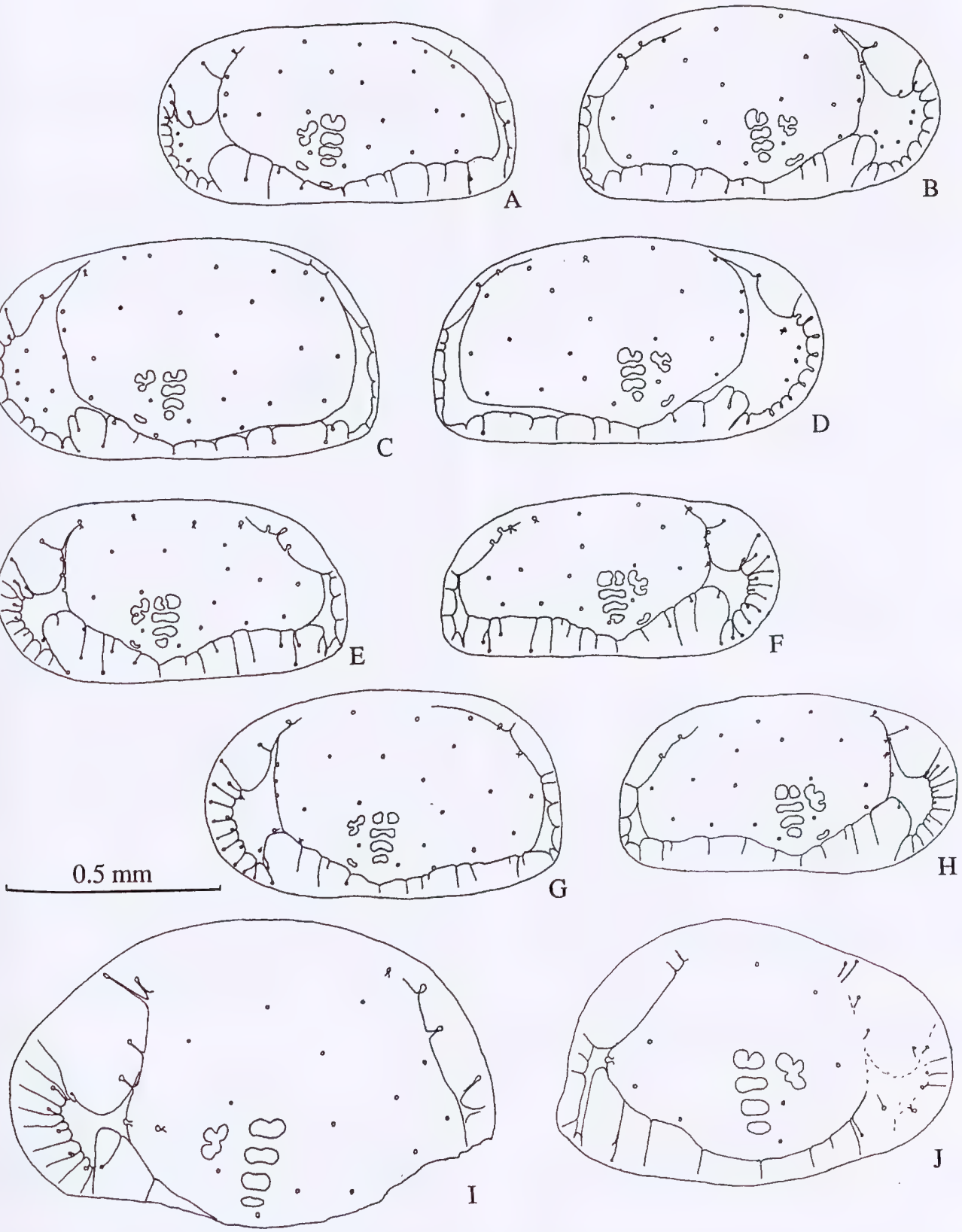

Figure 6. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, *Krithe dilata* n.sp., A, male left valve (ANU 57016), 105GC20, coretop, B, female right valve (ANU 57033), 71GC44, 100 cm, C, female left valve (ANU 57032), 71GC44, 100 cm, D, female right valve (holotype, ANU 57031), 71GC44, 100 cm; E–H, *Krithe pseudocomma* n.sp., E, male left valve (holotype, ANU 57027), GR5/4, 6 cm, Holocene, F, male right valve (ANU 57028), GR5/4, 2 cm, Holocene, G, female left valve (ANU 57029), GR5/4, 2 cm, Holocene, H, female right valve (ANU 57030), GR5/4, 4 cm, Holocene; I, J, *Krithe* sp. 2, I, female left valve (ANU 57064), TL8758, coretop, J, female right valve (ANU 57065), 12/87 12GC9, 65 cm.

interval 1.00–1.01 m; ANU 57016, length 0.91 mm, height 0.45 mm, coretop 105GC20. Specimens from 71GC044 are late Pleistocene in age.

Type locality and horizon. Tasman Sea, off eastern Australia present day water depth 1321 m, AGSO core 71GC044, interval 1.00–1.01 m, latest Pleistocene.

Diagnosis. A large, subrectangular species of *Krithe* with weak sexual dimorphism. Males lower than females. Posterior margin very truncate with a very shallow posterior indentation. Inner lamella narrow posterodorsally. Anterior vestibulum mushroom-shaped, often with extremely wide proximal expansion. ADRPC of type 2B; AD 1 is usually a normal pore sometimes a short RPC, AD 3 and 4 are normal pores.

Description. Carapace moderately large and rectangular. Dorsal and ventral margins are straight and subparallel. Anterior margin regularly convex; posterior margin rounded dorsally, truncate ventrally with no median shoulder and only weakly indented. Normal valve overlap. Inner lamella narrow posterodorsally and mid ventrally, moderately wide elsewhere. Anterior vestibulum large and mushroom-shaped with variable neck width, usually wide. ARPC's are short. ADRPC of type 2B. AD 1 is usually a normal pore sometimes a short RPC. AD 3 and 4 are normal pores. Posterior vestibulum is very narrow but often expanded proximally. Muscle scars large, undivided.

Remarks. The species is most similar to *K. comma* n.sp. and *K. pseudocomma* n.sp. It differs from those species, however, in its more symmetrical and greatly expanded anterior vestibulum, and its undivided adductor scars. The Atlantic Palaeogene species *Krithe regulare* Coles *et al.*, 1994, is also very similar, despite the considerable difference in geographical locality and stratigraphical range. Morphologically, *K. dilata* differs in size, having a more rounded posterior and much less marked sexual dimorphism.

Distribution. A relatively shallow occurring species recorded in this study between 355 to 1321 m on the eastern Australian continental slope.

Stratigraphical range. Early Pliocene (NN 14) to Recent, based on core records of DSDP site 593.

Krithe pseudocomma n.sp.

Figs. 6E–H, 8Y,Z

Etymology. Latin, referring to the close resemblance of this species to *Krithe comma* n.sp.

Type material and dimensions. HOLOTYPE, ANU 57027, male LV, length 0.88 mm, height 0.44 mm. PARATYPES: ANU 57028, male RV, length 0.86 mm, height 0.40 mm, core GR 5/4, interval 2–4 cm; ANU 57029, female LV, length 0.90 mm, height 0.52 mm, core GR 5/4, interval 2–4 cm; ANU 57030, female RV, length 0.86 mm, height 0.45 mm, core GR 5/4, interval 4–6 cm; All specimens are Holocene in age.

Type locality and horizon. Challenger Plateau, present day water depth 686 m, GRAINZ core 5/4, interval 2–4 cm, Holocene.

Diagnosis. A large, subrectangular species of *Krithe* with weak sexual dimorphism. Males lower than females. Posterior margin very truncate with a very shallow posterior indentation. Inner lamella wide posterodorsally. Anterior vestibulum crescentic, with distinct ventral distal expansion. ADRPC of type 2B; AD 3 and 4 are normal pores. The uppermost adductor scar is subdivided.

Description. Carapace large, strongly inflated, weakly sexually dimorphic, males lower than females. Dorsal margin straight to slightly convex and parallel with ventral margin, which is very slightly concave. Posterior margin truncate with shallow indentation. Normal overlap. Inner lamella moderately wide. Anterior vestibulum hook-shaped with variable neck width, strongly distally expanded ventrally. ARPC's are moderately long. ADRPC of type 2B. AD 1 is a short RPC or normal pore, AD 3 and AD 4 are normal pores. Posterior vestibulum is narrow. Muscle scars large, the upper adductor is subdivided.

Remarks. Internal carapace features of this species are similar to those of *K. comma* n.sp. as are certain aspects of its external morphology. However, there is a slight difference in ADRPC pattern: *K. pseudocomma* has an ADRPC of type 2B since AD 3 and AD 4 are always normal pores, whereas in *K. comma* AD 3 is usually a short RPC and, therefore, has an ADRPC of type 2A. Moreover, *K. pseudocomma* differs significantly from *K. comma* in its more cylindrical shape and its ventral distally expanded anterior vestibulum.

Distribution. Occurs only on the Lord Howe Rise and Challenger Plateau, ranging in depth from 686 to 1389 m.

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 207, 284, 592 and 593.

Krithe sp. 2

Figs. 6I,J, 8AA

Description. Female carapace extremely large, well inflated and heavily calcified. Dorsal margin is strongly convex; ventral margin less so. Anterior margin strongly convex, weakly concave dorsally. Posterior margin very truncate with weak posterior indentation. Normal valve overlap. Inner lamella is wide anteriorly and posteriorly, moderately wide ventrally. Anterior vestibulum narrow and mushroom shaped. ARPC's are moderately long. ADRPC of type 2B. AD 2 is very long and very close to the dorsal margin. Posterior vestibulum very narrow. Muscle scars large and not subdivided.

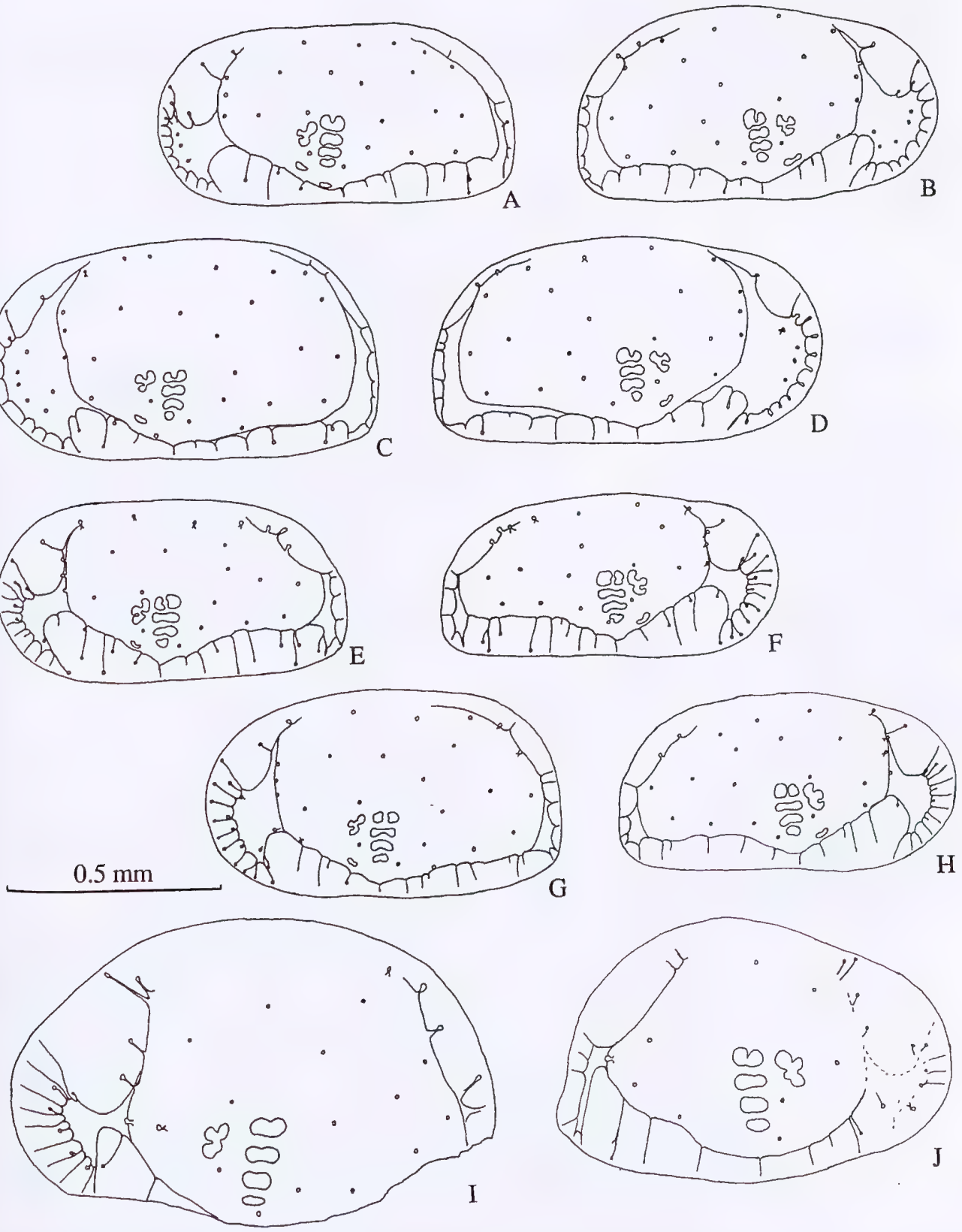

Figure 6. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, *Krithe dilata* n.sp., A, male left valve (ANU 57016), 105GC20, coretop, B, female right valve (ANU 57033), 71GC44, 100 cm, C, female left valve (ANU 57032), 71GC44, 100 cm, D, female right valve (holotype, ANU 57031), 71GC44, 100 cm; E–H, *Krithe pseudocomma* n.sp., E, male left valve (holotype, ANU 57027), GR5/4, 6 cm, Holocene, F, male right valve (ANU 57028), GR5/4, 2 cm, Holocene, G, female left valve (ANU 57029), GR5/4, 2 cm, Holocene, H, female right valve (ANU 57030), GR5/4, 4 cm, Holocene; I, J, *Krithe* sp. 2, I, female left valve (ANU 57064), TL8758, coretop, J, female right valve (ANU 57065), 12/87 12GC9, 65 cm.

Remarks. Only a few poorly preserved, probably female, specimens were found. In overall morphology they resemble *K. trinidadensis* but the ADRPC pattern is very different.

Distribution. Found at 1545 to 3281 m on the flanks and plateau of the Lord Howe Rise.

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 208.

ADRPC TYPE 3

Krithe morkhoveni morkhoveni Bold, 1960

Figs. 7A–C, 8DD,EE

For comprehensive pre-1988 synonymy see Coles *et al.* (1994).

Krithe morkhoveni Bold, 1960: 160; pl. 3, fig. 6.
Krithe sp. 11 Whatley & Zhao, 1993: fig. 3.11.
Krithe undecimradiata Ruggieri; Abate, Barra, Aiello & Bonaduce, 1993: 364; pl. 5, figs. 1–3.
Krithe morkhoveni morkhoveni Bold; Coles, Whatley & Moguilevsky, 1994: 94; pl. 3, figs. 11–18, text-fig. 4D–H.

Remarks. This species is significantly smaller (see Fig. 9) than the very similar species *K. trinidadensis*.

Distribution. A species common on the Continental Slope of Australia, recorded from 804 to 3552 m, but almost absent elsewhere in the Tasman Sea being found only at one site at 1125 m on the Challenger Plateau.

Stratigraphical range. Early Pliocene (NN 15) to Recent, based on core records of DSDP site 208 and GR5/4. It is known elsewhere from the Late Palaeocene onwards (Coles *et al.*, 1994), but in our Neogene cores from the Lord Howe Rise it is only very poorly represented.

Krithe pernoides sinuosa Ciampo, 1986

Figs. 7D–G, 8BB,CC

For comprehensive pre-1988 synonymy see Coles *et al.* (1994).

Krithe sinuosa Ciampo, 1986: 87; pl. 17, figs. 3, 5.
Krithe introcurva Hao in Ruan & Hao, 1988: 267; pl. 40, figs. 26–28.
Krithe pernoides (Bornemann); Abate, Barra, Aiello & Bonaduce, 1993: 362; pl. 2, figs. 8–11, pl. 3, fig. 13, pl. 6, fig. 10 (small form).
Krithe sp. 7 Whatley & Zhao, 1993: fig. 3.10.
Krithe pernoides sinuosa Ciampo; Coles, Whatley & Moguilevsky, 1994: 106; pl. 5, figs. 13–17, text-fig. 5R–V.

Distribution. Found only off eastern Australia restricted to a narrow depth range of 1274 to 1467 m.

Stratigraphical range. Early Pliocene (NN 14) to Recent, based on core records of DSDP sites 206 and piston cores on the Australian Continental Slope. The subspecies is known from the Early Miocene elsewhere (Coles *et al.*, 1994).

Krithe trinidadensis Bold, 1958

Figs. 2I,J, 7H–L, 8FF,GG

For comprehensive synonymy see Coles *et al.* (1994).

Krithe trinidadensis Bold, 1958: 398; pl. 1, figs. 3a, 3c,d, 3f, 6e.–Coles, Whatley & Moguilevsky, 1994: 99; pl. 4, figs. 7–12; text-fig. 4P–T, text-fig. 5A,B.

Remarks. The large size of this species (see Fig. 9) readily serves to distinguish it from the smaller, but otherwise very similar species, *K. morkhoveni morkhoveni* Bold.

Distribution. In coretop material we found this species only on the Continental Slope off Tasmania at a depth range of 1476 to 2346 m. Elsewhere in our study region it has been recorded rarely only as fossil in DSDP site 206, 3196 m in the New Caledonian Basin.

Stratigraphical range. Late Pliocene (NN 16) to Recent, based on core records of DSDP site 206. *Krithe trinidadensis* is known to occur from the Middle Eocene zone NP 16 (Coles *et al.*, 1994).

Discussion

Table 1 shows the depth distribution of all the species found in the two study regions, the East Tasman Sea (including the New Caledonia Basin, Lord Howe Rise and Challenger Plateau) and the Continental Slope off southern and eastern Australia. As in other parts of the world oceans greatest diversity occurs beyond 1,000 m in the bathyal and abyssal environment. In both our study areas some 15 species occur, or have occurred in the past. Not all of them, however, are common to both regions. Five species are absent from the Australian Continental Slope. They include *K. comma, K. pseudocomma, Krithe* sp. 2, these being confined to the plateau or flanks of the Lord Howe Rise; and *K. dolichodeira* and *K. minima*, which are geographically and bathymetrically widespread species, common, for example in the North Atlantic (Coles *et al.*, 1994). The absence from the slope regions of Australia of these two, otherwise cosmopolitan species, is perplexing. Three species, *K. posticliva, K. pernoides sinuosa*, and *K. trinidadensis* appear to have diminished their range, since they are recorded in modern sediments off Australia, but only in ancient sediments in the East Tasman Sea. Four other species, *K. dilata, K. perpulchra, K. prolata* and *Krithe* sp. 1, are restricted entirely to the Australian Continental Slope. Vertical range distribution of ubiquitous species likely relates to variations of vertical watermass structure and substrate type. The relatively steep-sided Australian Continental Slope offers only narrow areas of uniform watermass, and generally unstable, terrigenous rich

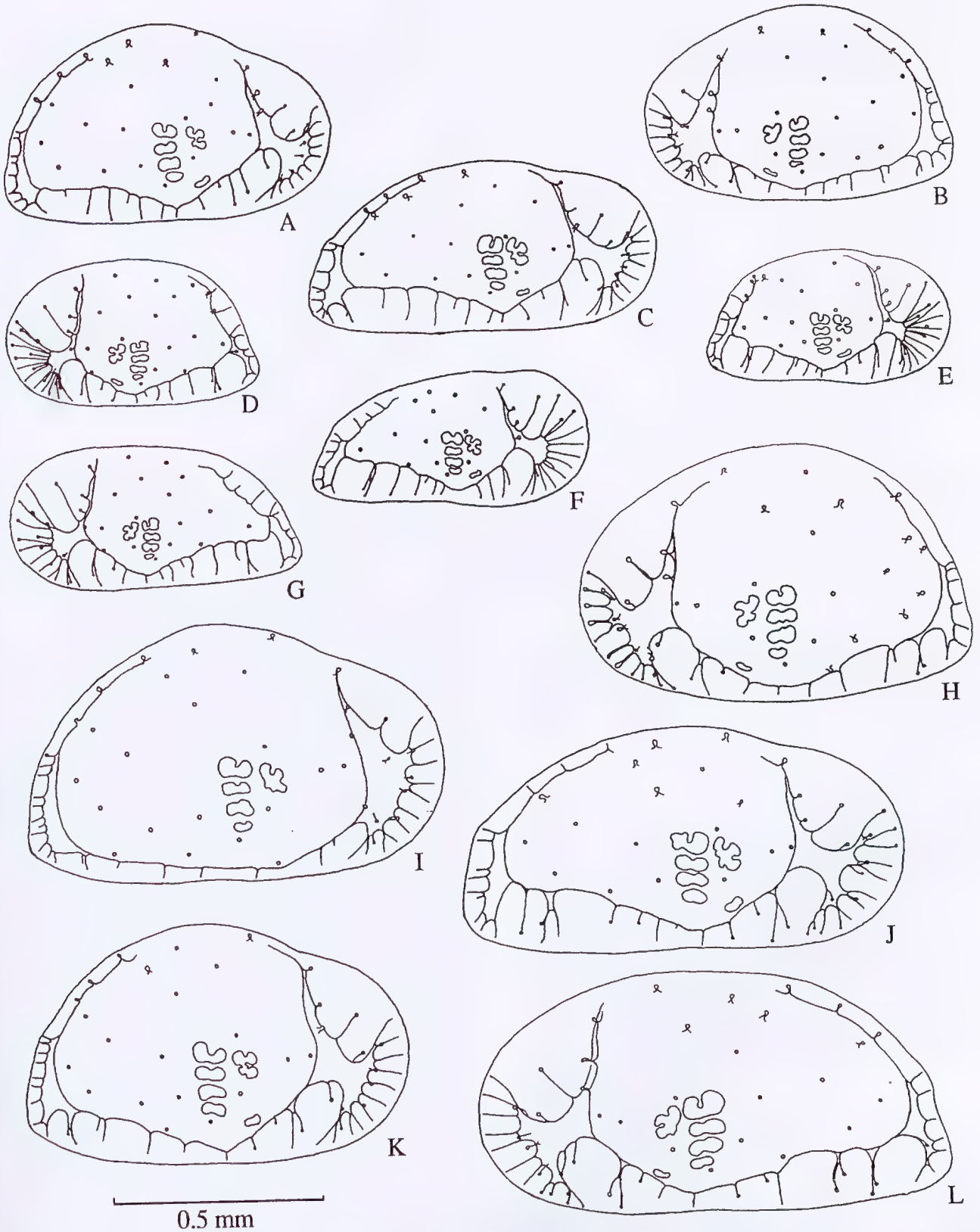

Figure 7. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–C, *Krithe morkhoveni morkhoveni* Bold, A, female right valve (ANU 57067), 9/86 Pc7, 84 cm, B, female left valve (ANU 57066), 67GC03, 25 cm, C, male right valve (ANU 57069), 67GC03, 107 cm; D–G, *Krithe pernoides sinuosa* Ciampo, D, female left valve (ANU 57070), 71GC44, 45 cm, E, female right valve (ANU 57071), 71GC44, 45 cm, F, male right valve (ANU 57073), 71GC44, 45 cm, G, male left valve (ANU 57072), 112GC9, coretop; H–L, *Krithe trinidadensis* Bold, H, female left valve (ANU 57074), 67GC03, 25 cm, I, female right valve, form with large anterior vestibulum (ANU 57075), 67GC03, 280 cm, J, male right valve (ANU 57078), 67GC03, 25 cm, K, female right valve (ANU 57076), 67GC03, 177 cm, L, male left valve (ANU 57077), 67GC03, 137 cm.

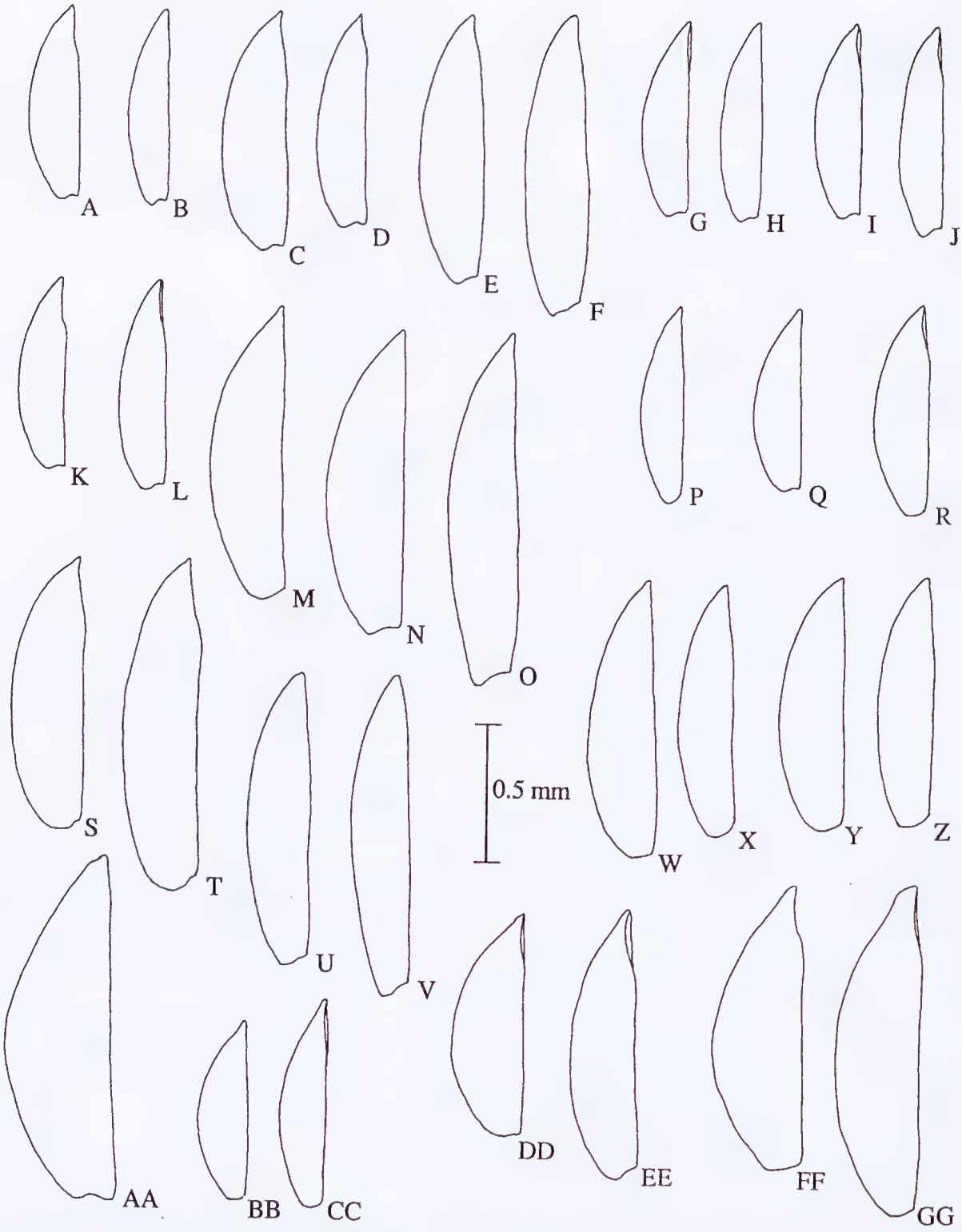

Figure 8. Camera lucida drawings of left valve profile in dorsal view. A, B, *Krithe compressa*, A, female, ANU 57035, B, male, ANU 57037; C, D, *Krithe antisawanensis*, C, female, ANU 57039, D, male, ANU 57044; E, F, *Krithe dolichodeira*, E, female, ANU 57043, F, male, ANU 57045, G, H, *Krithe marialuisae*, G, female, ANU 57047, H, male, ANU 57049; I, J, *Krithe minima*, I, female, ANU 57051, J, male, ANU 57053; K, L, *Krithe posticliva*, K, female, ANU 57055, L, male, ANU 57057; M, *Krithe reversa*, female, ANU 57034; N, O, *Krithe triangularis*, N, female, ANU 57013, O, male, ANU 57011; P, *Krithe* sp. 1, female?, ANU 57017; Q, *Krithe droogeri*, female, ANU 57059; R, *Krithe perpulchra*, female, ANU 57061; S, T, *Krithe prolata*, S, female, ANU 57021, T, male, ANU 57019; U, V, *Krithe comma*, U, female, ANU 57029, V, male, ANU 57024; W, X, *Krithe dilata*, W, female, ANU 57032, X, male, ANU 57016; Y, Z, *Krithe pseudocomma*, Y, female, ANU 57029, Z, male, ANU 57027; AA, *Krithe* sp. 2, female, ANU 57064; BB, CC, *Krithe pernoides sinuosa*, BB, female, ANU 57070, CC, male, ANU 57072; DD, EE, *Krithe morkhoveni morkhoveni*, DD, female, ANU 57066, EE, male, ANU 57068; FF, GG, *Krithe trinidadensis*, FF, female, ANU 57074, GG, male, ANU 57077.

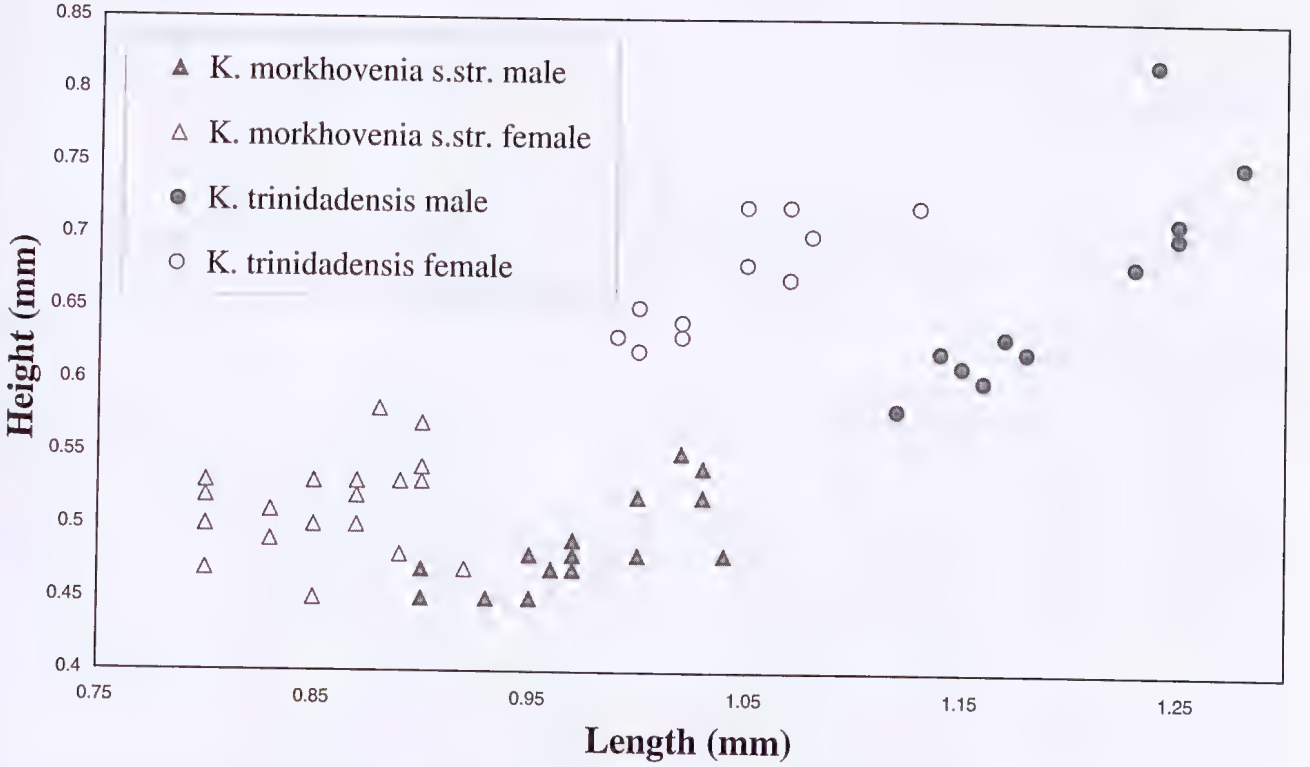

Figure 9. Size variation in adult *Krithe morkhoveni morkhoveni* and *Krithe trinidadensis*.

sediment regimes. Whereas the plateau regions of the eastern Tasman Sea are relatively stable, carbonate rich areas. These factors must have a profound influence upon the distribution of any benthonic living community.

Table 2 shows the stratigraphic ranges of all the species documented here. The success of the genus is striking, with a radiation throughout the Neogene from three species in the Early Miocene, to 19 by the Late Pleistocene. By comparison with the North Atlantic (Coles *et al.*, 1994), this diversity trend appears to be a global one. Of the seven species shared with the North Atlantic none appear at the same time in each ocean. Only two species, *K. minima* and *K. triangularis*, have earlier occurrences in the Southwest Pacific and, therefore, have probably evolved there. The Late Miocene to Late Pliocene saw the invasion of the Pacific of most of the Atlantic shared species. Further work is needed on Palaeogene occurrences in the Pacific to make further definite comparisons here concerning migration patterns and inter-oceanic correlation. It is clear, however, that the Pacific fauna consists of a mix of immigrant and endemic species. There exist species, characterised by ADRPC Type 2A (*K. comma*, and *K. pseudocomma*), that have remained in the Southwest Pacific region throughout their long, at least Miocene to Recent, range.

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Table 1. Bathymetric distribution of *Krithe* species and location details of sites considered in this report. ● = present; O = Lazarus occurrences; + = fossil occurrence only.

site	latitude S	longitude E	depth (m)	map code	*comma*	*pseudocomma*	*dolichodeira*	*antisawanensis*	*reversa*	*triangularis*	*minima*	*marialuisae*	*compressa*	*posticliva*	*droogeri*	*morkhoveni* s.str.	*Krithe* sp. 2	*pernoides sinuosa*	*trinidadensis*	*Krithe* sp. 1	*dilata*	*perpulchra*	*prolata*
Australian Continental Slope																							
AGSO 105GC20	26.502°	153.825°	355	41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	●	-	-
Fr5-91 41PC11	34.173°	151.603°	759	34	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	O	●	-
Fr5-91 40PC10A	34.352°	151.470°	773	28	-	-	-	-	-	-	-	-	O	-	-	-	-	-	-	-	●	●	-
Fr5-91 35PC9	35.538°	150.803°	804	27	-	-	-	-	-	-	-	-	●	-	-	●	-	-	-	-	●	-	-
Fr2/91 106C	36.993°	137.557°	835	1	-	-	-	-	-	-	-	-	O	-	-	●	-	-	-	-	O	-	-
AGSO 112/GC08	33.925°	151.858°	977	37	-	-	-	●	-	-	-	-	O	-	-	●	-	-	-	-	O	-	-
AGSO 71GC7	29.353°	153.875°	989	44	-	-	-	O	-	-	-	-	O	●	-	●	-	-	-	-	●	-	-
AGSO 105GC25	26.585°	153.852°	1022	42	-	-	-	O	●	-	-	-	O	O	-	O	-	-	-	-	O	-	-
Fr5-91 9GC9	34.150°	151.600°	1040	35	-	-	-	O	O	-	-	-	O	O	-	●	-	-	-	-	O	-	-
Fr1-91 24PC5	34.385°	151.515°	1048	30	-	-	-	●	O	-	-	-	O	O	-	●	-	-	-	-	O	-	-
AGSO 67/GC50	41.508°	144.290°	1081	21	-	-	-	●	O	-	-	-	O	O	-	O	-	-	-	-	O	-	-
AGSO 67/GC52	41.182°	143.958°	1145	19	-	-	-	●	O	-	-	-	O	O	-	O	-	-	-	-	O	-	-
AGSO 67/GC23	38.053°	139.932°	1146	5	-	-	-	●	O	-	-	-	O	O	-	O	-	-	-	-	O	-	-
AGSO 105GC13	25.255°	153.875°	1200	43	-	-	-	O	O	-	-	-	O	O	●	●	-	-	-	-	O	-	-
AGSO 67/GC32	39.668°	142.912°	1244	18	-	-	-	●	O	-	-	-	O	O	O	O	-	-	-	-	O	-	-
AGSO 67/GC02	37.398°	138.578°	1270	2	-	-	-	O	O	-	-	-	O	O	O	O	-	-	-	-	O	-	●
Fr9-86 PC7	34.325°	151.570°	1274	33	-	-	-	●	●	-	-	-	O	●	O	●	-	●	-	-	O	-	O
AGSO 71GC044	29.524°	153.900°	1321	45	-	-	-	O	O	-	-	-	●	●	●	●	-	●	-	-	●	-	O
Fr5-91 26PC7	34.505°	151.480°	1405	29	-	-	-	O	●	-	-	-	O	O	O	●	-	O	-	-	-	-	O
AGSO 67/GC33	39.758°	142.867°	1433	17	-	-	-	●	O	-	-	-	O	O	O	●	-	O	-	-	-	-	O
Fr5-91 19PC3	34.395°	151.532°	1458	31	-	-	-	O	O	-	-	-	O	O	O	●	-	O	-	-	-	-	O
AGSO 112GC9	33.950°	151.923°	1467	39	-	-	-	O	O	-	-	-	●	O	O	●	-	●	-	-	-	-	O
AGSO 67/GC03	37.550°	138.583°	1476	3	-	-	-	●	●	-	-	-	O	O	O	●	-	-	●	-	-	-	●
AGSO 67/GC17	38.287°	140.185°	1490	10	-	-	-	●	O	-	-	-	O	O	O	O	-	-	O	-	-	-	O
Fr2-91 163G	38.520°	140.544°	1523	13	-	-	-	●	●	-	-	-	O	O	O	●	-	-	O	-	-	-	O
AGSO 67/GC04	37.583°	138.583°	1526	4	-	-	-	O	O	-	-	-	O	O	O	●	-	-	●	-	-	-	●
E53-20	41.433°	144.102°	1533	20	-	-	-	●	●	-	-	-	O	O	O	●	-	-	O	-	-	-	-
AGSO 67/GC34	39.795°	142.813°	1630	16	-	-	-	●	●	-	-	●	O	O	O	O	-	-	O	-	-	-	-
AGSO 67/GC16	38.333°	140.182°	1650	9	-	-	-	O	O	-	-	●	O	O	O	●	-	-	O	-	-	-	-
Fr5-91 43GC11	34.102°	151.842°	1818	36	-	-	-	O	O	●	-	O	O	O	O	O	-	-	O	-	-	-	-
Fr2/91 162G	38.518°	140.411°	1880	12	-	-	-	●	●	O	-	●	O	O	O	●	-	-	O	-	-	-	-
Fr1-94 GR 1	46.251°	146.541°	1900	23	-	-	-	●	●	●	-	O	O	O	O	O	-	-	O	-	-	-	-
AGSO 67/GC15	38.382°	140.177°	1964	8	-	-	-	O	●	O	-	O	O	O	O	●	-	-	O	-	-	-	-
AGSO 71GC026	29.310°	154.067°	1989	46	-	-	-	●	●	●	-	O	O	●	●	●	-	-	O	-	-	-	-
Fr5-91 25PC6	34.425°	151.567°	1996	32	-	-	-	O	O	O	-	O	O	-	-	●	-	-	O	-	-	-	-
AGSO 112GC10	33.983°	152.000°	2007	40	-	-	-	O	O	O	-	O	O	-	-	●	-	-	O	-	-	-	-
AGSO 67/GC14	38.423°	140.165°	2250	6	-	-	-	O	●	O	-	●	O	-	-	●	-	-	O	-	-	-	-
E55-6	38.853°	141.063°	2346	14	-	-	-	●	●	●	-	●	O	-	-	●	-	-	●	-	-	-	-
AGSO 67/GC46	42.202°	144.413°	2360	22	-	-	-	O	O	O	-	O	●	-	-	●	-	-	-	-	-	-	-
Fr5/91 14PC1	34.125°	151.868°	2373	38	-	-	-	O	O	●	-	O	-	-	-	●	-	-	-	-	-	-	-
Fr2-91 161G	38.527°	140.210°	2450	11	-	-	-	●	●	O	-	●	-	-	-	●	-	-	-	-	-	-	-
E36-23	43.883°	150.050°	2521	26	-	-	-	●	●	●	-	-	-	-	-	●	-	-	-	-	-	-	-
AGSO 67GC/13	38.465°	140.167°	2525	7	-	-	-	O	●	O	-	-	-	-	-	●	-	-	-	-	-	-	-
Fr1/94 GC3	44.256°	149.991°	2667	25	-	-	-	●	●	●	-	-	-	-	-	●	-	-	-	-	-	-	-
AGSO 67/GC37	40.235°	142.425°	3090	15	-	-	-	●	O	O	-	-	-	-	-	O	-	-	-	-	-	-	-
TS 8925	28.240°	159.150°	3403	52	-	-	-	●	O	O	-	-	-	-	-	O	-	-	-	-	-	-	-
E27-30	45.067°	147.228°	3552	24	-	-	-	-	●	O	-	-	-	-	-	●	-	-	-	-	-	-	-
Fr1/86 24GC15	30.860°	156.790°	4470	48	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 1. Continued.

site	latitude S	longitude E	depth (m)	map code	*comma*	*pseudocomma*	*dolichodeira*	*antisawanensis*	*reversa*	*triangularis*	*minima*	*marialuisae*	*compressa*	*posticliva*	*droogeri*	*morkhoveni* s.str.	*Krithe* sp. 2	*pernoides sinuosa*	*trinidadensis*	*Krithe* sp. 1	*dilata*	*perpulchra*	*prolata*
East Tasman Sea																							
GR 5/4	41.152°	170.342°	686	72	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WB 95-3	40.218°	169.645°	850	71	●	O	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DSDP 284	40.508°	167.680°	1066	68	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
DSDP 593	40.508°	167.675°	1068	67	+	+	+	+	O	+	+	+	+	+	-	-	-	-	-	-	-	-	-
DSDP 592	36.473°	165.442°	1088	62	+	+	+	+	O	+	+	+	+	-	+	-	-	-	-	-	-	-	-
Q698	42.473°	169.133°	1100	69	●	O	O	O	●	O	O	O	O	-	O	-	-	-	-	-	-	-	-
WB 95-1	42.247°	169.508°	1125	70	●	●	●	●	●	●	●	●	O	-	O	●	-	-	-	-	-	-	-
RC9-128 TL 8731	36.130°	166.070°	1234	64	O	O	O	●	O	O	O	O	O	-	O	O	-	-	-	-	-	-	-
SO 36-61	30.550°	161.438°	1340	58	●	O	●	●	O	●	●	●	●	-	O	O	-	-	-	-	-	-	-
DSDP 207	36.963°	165.434°	1389	61	+	+	+	+	+	+	+	+	O	-	O	O	-	-	-	-	-	-	-
OSI 12-87 13GC10	29.258°	161.255°	1416	56	-	-	O	●	●	O	O	O	O	-	O	O	-	-	-	-	-	-	-
Z2108	33.376°	161.612°	1448	59	-	-	●	●	●	●	●	●	●	-	O	O	-	-	-	-	-	-	-
TL 8730	34.010°	167.540°	1533	66	-	-	O	●	O	O	O	O	O	-	O	O	-	-	-	-	-	-	-
OSI 1-86 6GC3	32.980°	159.998°	1540	54	-	-	●	●	●	O	●	●	●	-	O	O	-	-	-	-	-	-	-
DSDP 208	26.110°	161.221°	1545	55	-	-	+	+	+	+	+	+	+	-	O	+	+	-	-	-	-	-	-
TS 8648	28.080°	161.310°	1607	57	-	-	O	●	O	●	●	●	O	-	O	-	O	-	-	-	-	-	-
TL 8759	26.000°	154.540°	1942	47	-	-	●	O	O	O	O	O	O	-	O	-	O	-	-	-	-	-	-
Fr 1-86 19GC11	29.960°	159.841°	2067	53	-	-	●	●	●	O	O	O	O	-	O	-	O	-	-	-	-	-	-
TL 8646	28.120°	158.130°	2220	50	-	-	O	●	O	O	O	O	O	-	O	-	O	-	-	-	-	-	-
TS 8647	28.080°	158.190°	2253	51	-	-	O	●	O	O	O	O	O	-	O	-	●	-	-	-	-	-	-
TS 8656	33.320°	166.320°	2860	65	-	-	●	O	●	O	●	●	●	-	O	-	O	-	-	-	-	-	-
TL 8758	25.530°	157.520°	2930	49	-	-	O	O	O	O	O	-	●	-	O	-	●	-	-	-	-	-	-
DSDP 206	32.013°	165.453°	3196	63	-	-	+	+	+	O	+	-	O	-	+	-	O	+	+	-	-	-	-
Fr12-87 12GC9	27.387°	165.338°	3281	60	-	-	●	●	-	●	●	-	●	-	-	-	●	-	-	-	-	-	-

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Table 2. Stratigraphical distribution of the species described herein. Age in parenthesis indicates earliest known age of the species if older than that found in the present study. ● = present, O = Lazarus occurrences.

epoch	Early Miocene	Early Miocene	Early Miocene	Early Miocene	Early–Mid. Miocene	Mid. Miocene	Mid. Miocene	Mid. Miocene	Mid. Miocene	Late Miocene	Late Miocene	Late Miocene	Early Pliocene	Early Pliocene	Early Pliocene	Early Pliocene	Late Pliocene	Late Pliocene	Late Pliocene	Early Pleistocene	Late Pleistocene	Late Pleistocene	Recent
nannofossil NN zone	1	2	3	4	5	6	7	8	9	10	11a	11b	12	13	14	15	16	17	18	19	20	21	
K. minima	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	O	O	●	●	●	●
K. pseudocomma	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●	O	●	●	O	●	●	●	●
K. triangularis	●	O	O	●	●	●	●	●	●	O	O	O	●	●	●	O	●	●	O	●	●	●	●
K. antisawanensis	-	-	-	-	-	●	●	●	●	O	●	●	●	●	●	●	●	●	●	●	●	●	●
K. comma	-	-	-	-	-	●	O	O	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
K. droogeri	-	-	-	-	-	●	O	O	O	O	O	O	O	O	O	●	O	O	O	O	O	●	●
K. marialuisae	-	-	-	-	-	-	●	●	O	O	O	●	●	●	●	●	●	O	O	●	●	●	●
K. compressa	-	-	-	-	-	-	-	-	-	-	●	●	●	●	O	O	●	●	●	●	●	●	●
K. dolichodeira	-	-	-	-	-	-	(Early Eocene, NP 10)					●	●	●	●	●	●	O	O	●	●	●	●
K. reversa	-	-	-	-	-	-	-	- (Middle Miocene, NN 6)						●	●	●	●	●	O	●	●	●	●
K. dilata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	O	O	O	O	O	O	●	●
K. pernoides sinuosa	-	-	-	-	-	-	-	-	-	(Early Miocene, NN 5)					●	●	●	O	O	●	●	●	●
K. morkhoveni s.str.	-	-	-	-	-	-	-	-	-	- (Late Palaeocene, NP 7)					●	●	●	O	O	●	●	●	●
K. posticliva	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	●	●	O	O	●	●
K. trinidadensis	-	-	-	-	-	-	-	-	-	-	- (Middle Eocene, NP 16)						●	O	O	O	O	●	●
Krithe sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	●	●	●	●	●	●
Krithe sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	O	O	●
K. perpulchra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- (Late Pliocene, NN 16)						●	●
K. prolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	●

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Two Solenogaster Molluscs, *Ocheyoherpia trachia* n.sp. from Macquarie Island and *Tegulaherpia tasmanica* Salvini-Plawen from Bass Strait (Aplacophora: Neomeniomorpha)

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ABSTRACT. *Tegulaherpia tasmanica* Salvini-Plawen is herein redescribed and illustrated from 22 individuals collected in Bass Strait and expands the original text diagnosis to include illustrations. Similarities between *Tegulaherpia*, which belongs to the Lepidomeniidae, and the written description and figures of *Lepidomenia hystrix* Marion & Kowalevsky, the nominate species for which there is no known type, suggests synonymy.

Nineteen individuals of *Ocheyoherpia trachia* n.sp. were collected at diving depths from Macquarie Island. It is the second species to be described in the previously monotypic subantarctic genus *Ocheyoherpia* Salvini-Plawen and differs from *O. lituifera* in its shorter epidermal spicules, dorsal carina, size of radula, number of copulatory spicules and their relationship to the large copulatory spicule glands, a large dorsal sinus, and thin cuticle. Familial status is shown to be uncertain.

In both *T. tasmanica* and *O. trachia* the morphology of hard parts (epidermal spicules, radula, and copulatory spicules) is emphasized. The reproductive system is described for *T. tasmanica* and remarks made on differences in the reproductive systems of the two *Ocheyoherpia* species.

SCHELTEMA, AMÉLIE H., 1999. Two solenogaster molluscs, *Ocheyoherpia trachia* n.sp. from Macquarie Island and *Tegulaherpia tasmanica* Salvini-Plawen from Bass Strait (Aplacophora: Neomeniomorpha). *Records of the Australian Museum* 51(1): 23–31.

The continental shelf and offshore benthos of Australia affords numerous species of Aplacophora (Scheltema, 1998). This short contribution to the benthos of Bass Strait and Macquarie Island is part of a continuing series of descriptions of Australian aplacophoran species.

Seldom have neomenioid aplacophorans—those that creep about on a narrow, ventral ridgelike foot—been described by placing emphasis on hard-part and external morphologies, although these are characters most readily available for identification. They are a focus of this paper in the certitude that the taxonomy of Aplacophora can be made available to more than the specialist.

Materials and methods

The species described are from collections made during the Macquarie Island Expedition 1977–78 (Australian Museum) and Bass Strait Survey 1979–1984 (National Museum of Victoria). Holotypes, paratypes, and voucher specimens are deposited in or were borrowed from the Australian Museum (AM), Museum of Victoria (MV), Tasmanian Museum (TM), and the National Museum of Natural History, Washington, DC (USNM).

Holotypes were drawn under a dissecting microscope with the aid of an ocular drawing tube and then photographed. The drawings emphasize spicule attitude and details of the anterior and posterior ends. Measurements were made by a map wheel or by dividers on drawings: *length* is the axial midline of a specimen in lateral view, *height* is the dorsoventral diameter, and *width* the lateral diameter. Epidermal spicules and radulae were treated as in Scheltema (1989), with the exception that radulae were mounted in CMCP-10©, a water-miscible mountant. To obtain isolated copulatory spicules, the posterior end of an individual was cut off and the tissue dissolved in hypochlorite solution (household bleach). A permanent slide was prepared by washing spicules with distilled water and transferring them to a slide with the aid of a micropipetter. After air-drying, a mountant and coverslip were added. Measurements of radulae, epidermal spicules, and copulatory spicules were made with an ocular micrometer. Histologic sections were paraffin embedded and cut at 7 µm or epon embedded and cut at 1.5 µm. The former were stained by hematoxylin and Gray's double contrast or by Mallory-Heidenhain trichrome; epon sections were stained with azure II and methylene blue.

The general anatomy of Neomeniomorpha has been described by Salvini-Plawen (1985a), Scheltema *et al.* (1994), and Scheltema (1998). The arrangement of epidermal spicules are: (*a*) *skeletal*, lying within the cuticle at right angles to each other in one or more layers spiralled from ventroanterior to dorsoposterior and from dorsoanterior to ventroposterior; (*b*) *upright*, more or less erect in a single layer, or (*c*) *adpressed*, with a single layer of overlapping spicules flat against the body wall cuticle. Species may have one or more spicule arrangements and one to several spicule morphologies. Spicules are formed of aragonite; they may be hollow or solid throughout. The radula of neomenioids is *distichous* (two teeth per row), *monostichous* (one tooth per row), or *polystichous* (many teeth per row); it is lacking in 20 percent of known species. Neither distichous nor polystichous radulae have a central, median tooth like the rachidians in gastropod radulae. In distichous radulae the denticles may be borne on a bar attached entirely or partially to the radular membrane, or they may be denticulate hooks largely free of the membrane. In distichous bars, the largest denticles are lateral. During growth denticles are added to new teeth either medially or by bifurcation of a pre-existing denticle.

Species descriptions

Neomeniomorpha Pelseneer, 1906

Ventroplicida Boettger, 1956; Solenogastres Gegenbaur, 1878 [*partim*], Salvini-Plawen, 1967. *Non* Neomeniamorpha Salvini-Plawen, 1978.

Diagnosis. Aplacophoran molluscs with a narrow footfold in a ventral, longitudinal pedal groove and without a cuticular oral shield or mantle cavity ctenidia; midgut as a combined stomach and digestive gland; monoecious.

Remarks. A ventral groove in a spicule-covered, vermiform organism identifies it as a neomenioid mollusc.

Family Lepidomeniidae Pruvot, 1902

Type genus. *Lepidomenia* Kowalevsky in Brock, 1883 (1992, *Bull. Zool. Nomen.* 49: 158, Op. 1676).

Diagnosis. Epidermal spicules thin, platelike, adpressed; cuticle thin; radula small, with distichous hooks (Fig. 3B); ventral salivary glands paired, tubular, opening through paired ducts.

Remarks. With three genera of small neomenioids, *Lepidomenia* Kowalevsky, 1883, *Nierstraszia* Heath, 1918, and *Tegulaherpia* Salvini-Plawen, 1983.

Tegulaherpia Salvini-Plawen, 1983

Type species. *Tegulaherpia stimulosus* Salvini-Plawen, 1983, by monotypy [corrected to *T. stimulosa* (Salvini-Plawen, 1988)].

***Tegulaherpia* distribution**. Bass Strait (Australia), Mediterranean Sea, Irish Sea, Norwegian fjords, between 50 and 470 m (Salvini-Plawen, 1983, 1997).

Diagnosis. Slender, < 5 mm long, shiny, epidermal spicules quadrate, foot not within groove, mouth separate from vestibule, without midgut sacculations, with seminal vesicles, without seminal receptacles, paired lower gametoducts either united or joined laterally to anterior extension of mantle cavity, paired copulatory spicules 2 per sac, dorsoterminal sense organ rudimentary above large, granule-filled epidermal cells.

Remarks. Species of *Tegulaherpia* were placed provisionally in the Lepidomeniidae on the basis of a thin cuticle with scales, a distichous radula, and what is here called tubular ventral salivary glands (Salvini-Plawen, 1988, as subepithelial-follicular glands). The nominate genus of the family is monotypic, based on the description of a single juvenile individual from the Mediterranean, *L. hystrix*

Marion & Kowalevsky. No Aplacophora has since been attributed either to *L. hystrix* or to the genus *Lepidomenia* with certainty, although six individuals of *L. hystrix* were reported, without description, from the type locality (Swedmark, 1956; Salvini-Plawen, 1985b). Suggested here is that the genus *Tegulaherpia* may be synonymous with *Lepidomenia* based on similarities between the written description and figures of *L. hystrix* (Kowalevsky & Marion, 1887) and those of *T. tasmanica*, described below, which in turn is similar to *T. stimulosa* from the Mediterranean (Salvini-Plawen, 1988).

Tegulaherpia tasmanica Salvini-Plawen, 1988

Figs. 1, 2, 3A,B

Tegulaherpia sp.–Scheltema, 1998, fig. 2.8

Type material. Holotype (TM, E23218) and paratypes, Tasmanian Museum, Hobart.

Type locality. Off northern coast of Tasmania between Burnie and Penguin, 50–55 m.

Vouchers. Bass Strait, Australia, 39°48.6'S 146°18.8'E, 82 m (RV *Tangaroa* BSS-S 158 [epibenthic sled], 13.xi.81): MV 83492 (entire alcohol specimen, spicule slide); length 3.6 mm; anterior, midbody, and posterior height 1.0, 0.5, and 0.3 mm, respectively; width 0.3, 0.4, and 0.3 mm; MV 83493 (dissected alcohol specimen; radula, spicule slides).

Material examined. 22 individuals, including 2 paratypes from off Tasmania and 20 individuals from Bass Strait Survey, RV *Tangaroa*, November 1981: 2, BSS-S 157 (epibenthic sled), 40°10.9'S 145°44.3'E, 75 m; 7, BSS-S 158 (epibenthic sled), 39°48.6'S 146°18.8'E, 82 m; 2, BSS-S 159 (epibenthic sled), 39°46.0'S 146°18.0'E, 80 m; 1, BSS-G 159 (Smith-MacIntyre grab), 39°43.5'S 146°18.8'E, 80 m; 5, BSS-S 165 (epibenthic sled), 40°13.8'S 148°39.6'E, 60 m; 3, BSS-S 169 (epibenthic sled), 39°02.4'S 148°30.6'E, 120 m.

Description. Up to 3.7 mm long, greatest height anterior, to 1.0 mm, tapered posteriorly, posterior height to 0.4 mm, somewhat compressed laterally, midbody height to 0.7 mm, width to 0.5 mm, anterior end rostrate, posterior end somewhat pointed to rounded, ventral line indicated by erect spicules on each side of foot (Figs. 1A, 3A); contracted mouth opening Y-shaped with a small knob in fork of the Y; contracted pedal pit opening distinct, laterally slit-shaped (Fig. 1B); mantle cavity opening terminal (Fig. 1C), dorsoterminal sense organ not externally obvious. Cuticle thinner than epidermis, 5 and 10 µm, respectively; epidermis with thickset, heavily granulated papillae. Epidermal spicules about 1 µm thick, of four types, all with small, sharp distal point; most numerous spicules quadrate (Fig. 1, spicule D1), widest at base, base laterally concave and medially straight, to 42 µm long by 29 µm wide; type 2 (spicule D2) short, symmetrical paddles to 42 µm long by 14 µm wide, ending basally in a small knob; type 3 (spicules D3) large, asymmetrical paddles, convex on one side, flat to slightly convex on the other, with basal knob, to 75 µm long by 15 µm wide; and type 4 (spicule D4) large, asymmetrical ovoid spicules lateral to foot spicules, base narrow, straight, to 57 µm long by 26 µm wide; variation within each spicule type slight; spicules from beside foot (spicules D5) both with and without narrow handle on truncated base, spicule convex next to handle, becoming concave distally, convex on opposite side, to 52 by 15 µm not including handle. Radula (2 examined) with about 15 rows; teeth with 4 median denticles and distal hook, base produced into additional denticle-like protuberance, to 53 µm long (Figs. 1G,H, 3B). Copulatory spicules examined from one individual with 2 long, slender spicules of about equal length per sac, one fitting into a groove in the other, sharply pointed and slightly curved distally, proximally rounded and, in one of the two spicules, slightly bulbous; 700 µm long, greatest width 20 µm (Fig. 1E,F).

Reproductive system. *Tegulaherpia tasmanica*, like *T. stimulosa*, has paired seminal vesicles opening off the anterior end of the gonopericardial ducts but no seminal receptacles (Fig. 2A,B). The lower gametoducts remain paired, opening laterally onto a dorsoventrally compressed tubular extension of the mantle cavity, as indicated by cell contents (Fig. 2C,D); further posteriorly the epithelium of the gametoducts joins ventrally but not dorsally. Copulatory spicules are formed before maturation of gonad primordium in juveniles (Fig. 2D).

Remarks. The illustrated description here expands the original written diagnosis of the species (Salvini-Plawen, 1988); identifications were made by comparisons with paratype material. For differences between *Tegulaherpia tasmanica* and the two other *Tegulaherpia* species, *T. stimulosa* and *T. myodoryata* Salvini-Plawen, I have relied on the original descriptions. In body shape, the anterior end of *T. tasmanica* is pointed, not rounded (cf. Figs. 1A, 3A with Salvini-Plawen, 1988, figs. 7, 8). The description of *T. stimulosa* from the Mediterranean, which *T. tasmanica* most closely resembles, does not include illustrations of all types of epidermal spicules or the copulatory spicules. According to the written description, in *T. stimulosa* the spicules from beside the foot are smaller and pedal glands less distinct than I observed in *T. tasmanica*, and ducts of the salivary glands are ampulla shaped, rather than tubular as in *T. tasmanica*. According to the written description of *T. tasmanica* (Salvini-Plawen, 1988, p. 385) there are anatomical differences between the two species in the relationships of the rectum and copulatory spicule sheaths and their openings into the mantle cavity. The statement that there is an unpaired portion of the lower gametoduct longer than in *T. stimulosa*, however, is not in accord with my observations, that the lower gametoducts remain paired and open laterally onto an extension of the mantle cavity (Fig. 2C,D). It is perhaps the mantle cavity extension that is longer in *T. tasmanica*.

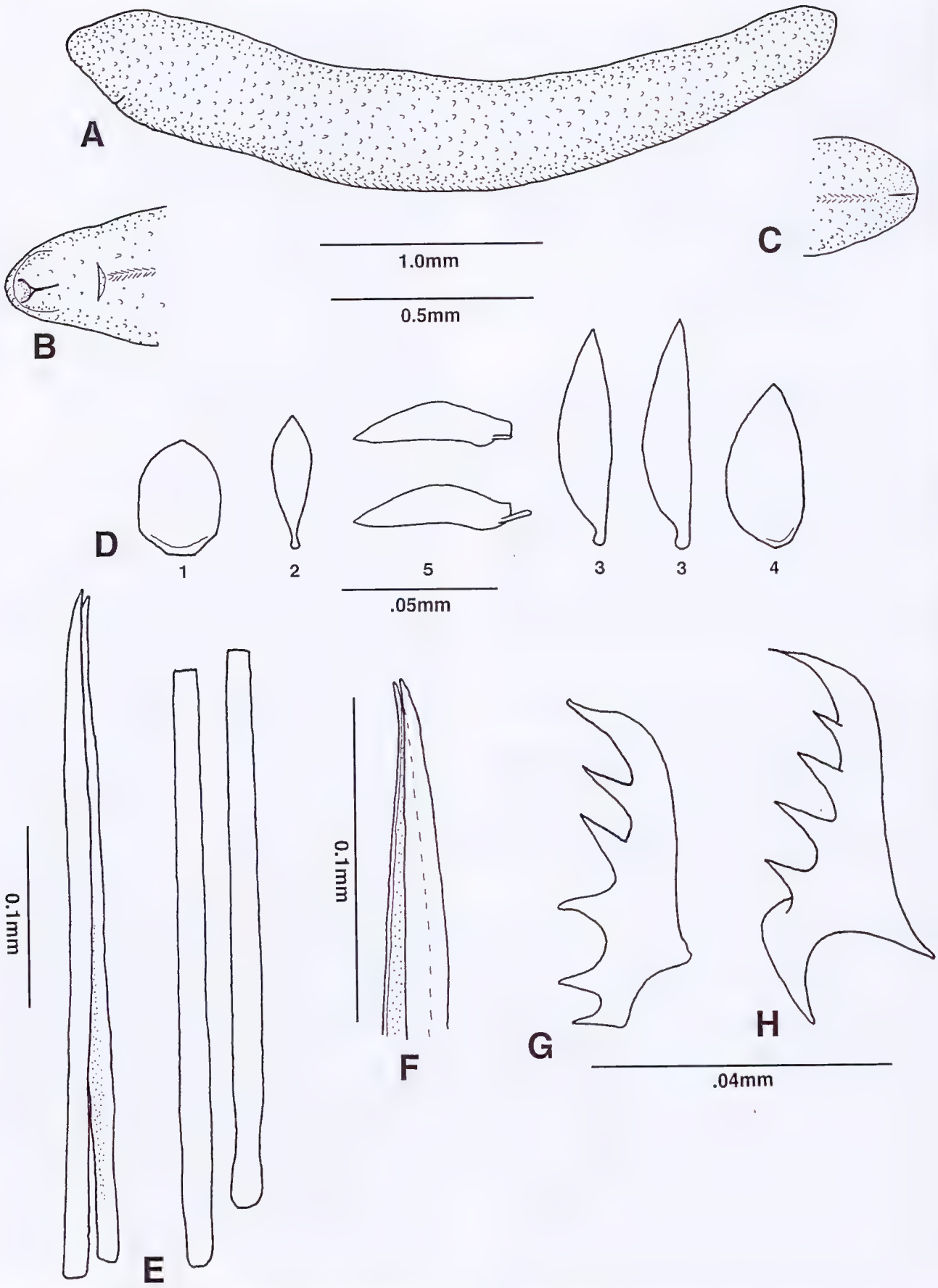

Figure 1. *Tegulaherpia tasmanica* Salvini-Plawen. A–C, voucher specimen (MV 83492): A, anterior to left, upper scale; B, C, ventral views of anterior and posterior ends, respectively, lower scale. D, epidermal spicules of A, types 1–5. E, F, copulatory spicules, basal portions to right in E broken off from pointed distal portions to left; stippling indicates groove. G, H, oldest and second newest radular teeth. E–H from dissected voucher specimen (MV 83493).

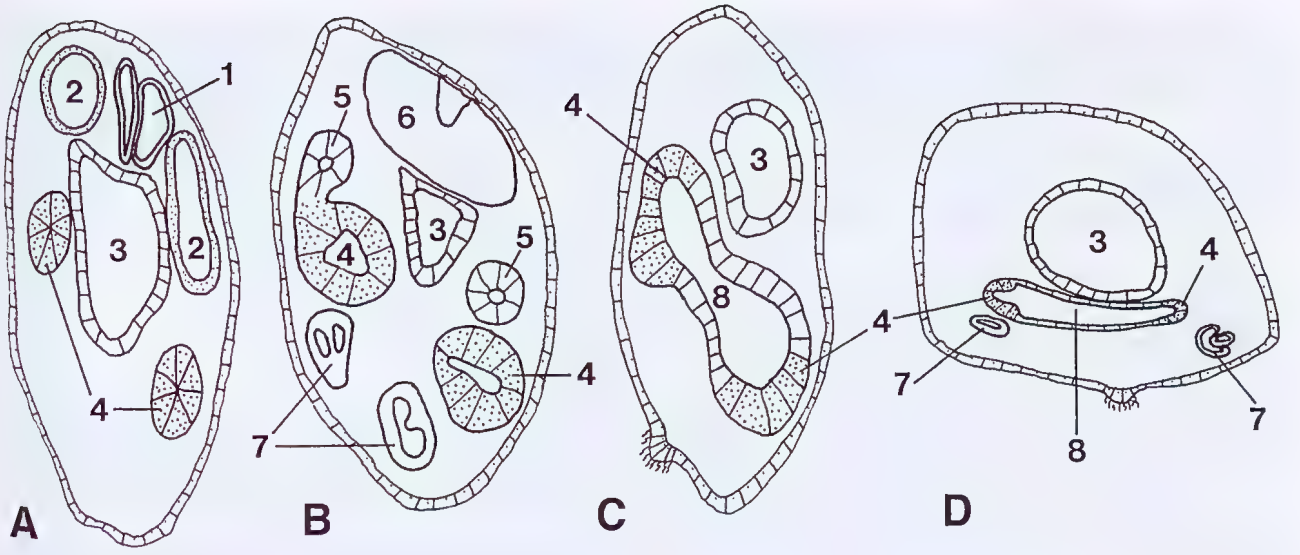

Figure 2. *Tegulaherpia tasmanica* Salvini-Plawen, reproductive system; semischematic drawings of sectioned material. A–C, mature individual from same location as voucher specimen. D, paratype, immature individual. Foot indicated in C and D only; missing copulatory spicule sacs in section C an artifact of sectioning. 1 gonopericardial duct, 2 seminal vesicle, 3 intestine, 4 lower gametoduct (blind ends shown in section A), 5 upper gametoduct, 6 pericardium with heart, 7 copulatory spicule sac, 8 anterior extension of mantle cavity.

Family incertae sedis

Ocheyoherpia Salvini-Plawen, 1978

Type species. *Ocheyoherpia lituifera* Salvini-Plawen, 1978, by monotypy.

***Ocheyoherpia* distribution**. Off subantarctic islands (South Sandwich, South Shetland, and South Georgia) at depths less than 250 m; Macquarie Island at less than 15 m depth.

Diagnosis. Thick-bodied, small neomenioids with solid epidermal spicules in the form of spines, barbed spicules, and serrated spicules; skeletal spicules lacking; cuticle thick or thin; with two pairs of pharyngeal salivary glands, one of them acinar; radular teeth with several denticles on a bar incompletely attached to radular membrane, outer denticles fused to a curved process swung from beneath tooth base; dorsal midgut coecum paired; midgut sacculate; copulatory spicules 2 or more per pair; paired seminal receptacles and accessory copulatory glands present; gametopore single; respiratory folds low, few; dorsoterminal sense organ absent.

Remarks. Assignation of the genus *Ocheyoherpia* to the Phyllomeniidae (Salvini-Plawen, 1978) seems untenable on these grounds: (*a*) *Ocheyoherpia* spp. do not have true gametoducts as uniquely held by species of *Phyllomenia* (Salvini-Plawen, 1978); (*b*) both barbed epidermal spicules and spines are solid and, in contradistinction to the original description and unlike Phyllomeniidae, skeletal spicules are lacking (Fig. 3D); and (*c*) the radular teeth have the form of a bar with denticles, unlike the distichous hooks of Phyllomeniidae.

Ocheyoherpia lituifera Salvini-Plawen, 1978

Figs. 3C, 5A,B

Type material. HOLOTYPE: USNM 749738 (alcohol specimen, spicule slide). 3.7 mm long, midbody height 0.7 mm. PARATYPE: USNM 749739 (histologic sections); off South Shetland Island, 62°41'S 54°43'W, 210–220 m (U.S. Antarctic Res. Pgm. stn 12-1003, 15.iii.64).

Type locality. Off South Sandwich Island, 56°19–20'S 27°28–29'W, 148–201 m (U.S. Antarctic Res. Pgm. 1961–1972, stn 22-1581, 6.iii.1966).

Diagnosis. Spiny (Fig. 3C) (see also Salvini-Plawen, 1978, fig. 288), cuticle thick (56 μm), epidermis thin (22 μm); spinelike epidermal spicules thick, long and wide, many greater than 160 μm long and up to 16 μm wide with an untapered, flat base (Fig. 5A); barbs to 170 by 14 μm; distally serrated spicules to 225 μm (see Salvini-Plawen, 1978, fig. 92); short scimitar-like spicules common. Radular teeth approximately 40 μm in length, tips of lateral, fused denticles curved in histologic sections (Fig. 5B). Form of copulatory spicules not known.

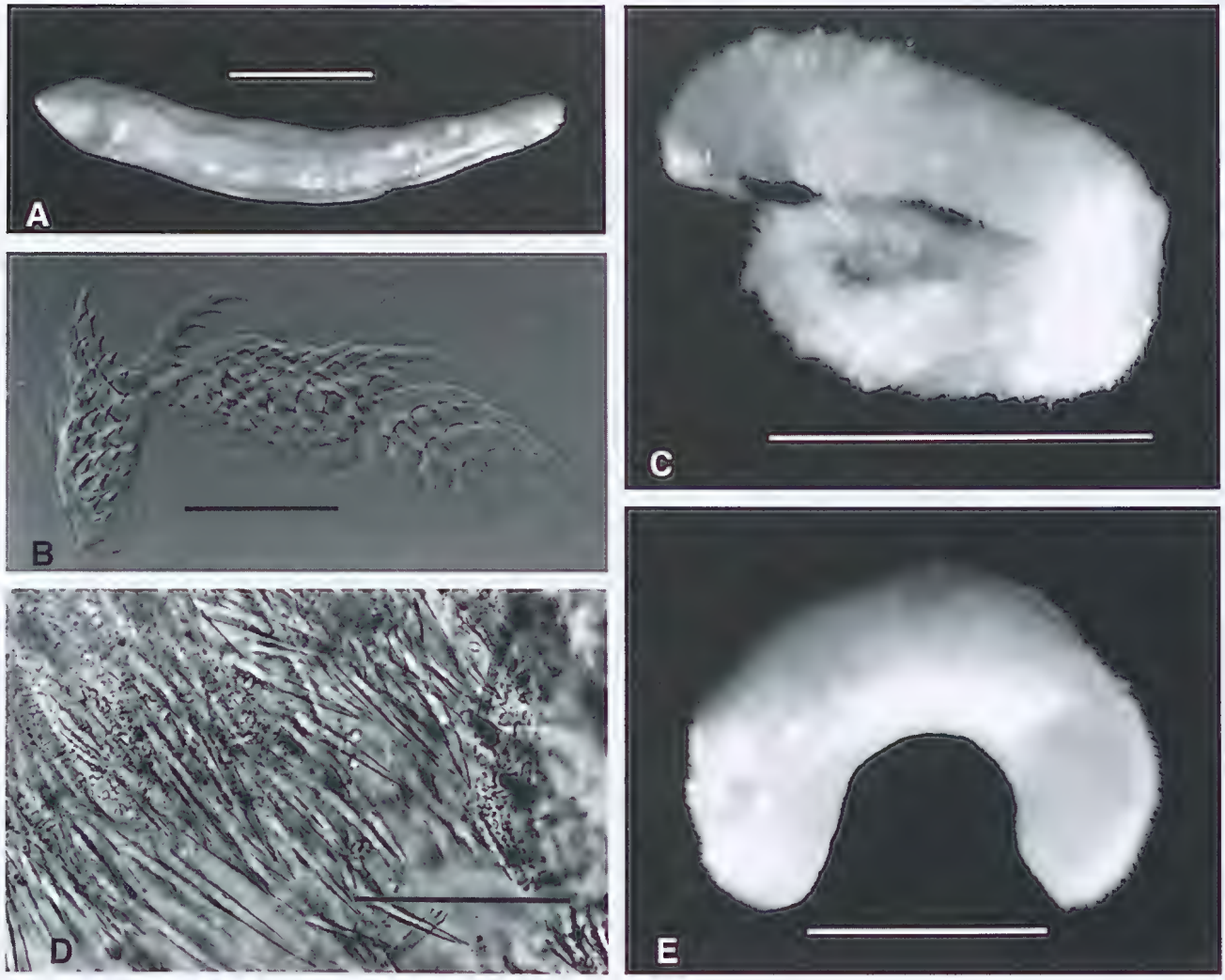

Figure 3. A, B, *Tegulaherpia tasmanica* Salvini-Plawen: A, voucher specimen (MV 83492); B, distichous radula from a Bass Strait individual (RV *Tangaroa* BSS-S 165). C, *Ocheyoherpia lituifera* Salvini-Plawen, holotype, with mantle cavity partially open (USNM 749738). D, E, *Ocheyoherpia trachia* n.sp.: D, epidermal spicules viewed from beneath cuticle; upright spicules only, without skeletal spicules; E, holotype (AM C203646). Anterior to left, dorsal above in A, C, E.

Ocheyoherpia trachia n.sp.

Figs. 3D,E, 4, 5C–F

Ocheyoherpia sp.–Scheltema *et al.*, 1994, figs. 8A,C, 20G; Scheltema, 1998, fig. 2.15.

Type material. HOLOTYPE: AM C203646 (alcohol specimen, spicule slide); length 5.4 mm, anterior, midbody, and posterior height 1.1 mm. PARATYPES (21): AM C203647 (dissected alcohol specimen, radula slide, epidermal and copulatory spicule slides), type locality; AM C203648 (dissected alcohol specimen), type locality. A further 19 paratypes from Macquarie Island Expedition not dissected: 3, Green Gorge Reef, vertical rock wall, 6.1 m (stn MA-275, 54°38'S 158°55'E, AM C149632); 12, rocks, Garden Bay Peninsula, 11 m (AM C149633, type locality); 2, Green Gorge, boulders on sand-gravel bottom, 14 m (stn MA-245, 54°38'S 158°55'E, AM C149634); 1, off Garden Bay Peninsula, rocks, 11–14 m (stn MA-128, 54°30'S 158°57'E, AM C149635); 1, Green Gorge, boulders on sand and gravel bottom, 13.7 m (stn MA-247, 54°38'S 158°55'E, AM C149636) (histologic sections).

Type locality. Macquarie Island, from Garden Bay Peninsula, vertical rock face, 11 m (Australia Museum Macquarie Island Expedition 1977–78, stn MA-125, 54°30'S 158°57'E, 16.xii.1977).

Diagnosis. Length to 6.5 mm; spicular coat rough, not shiny; with dorsal carina; barbed spicules few; serrated spicules few, anterior only; two deeply curved copulatory spicules per copulatory spicule sac, the shorter one with grooves and ridges on distal half; cuticle thin (22 m).

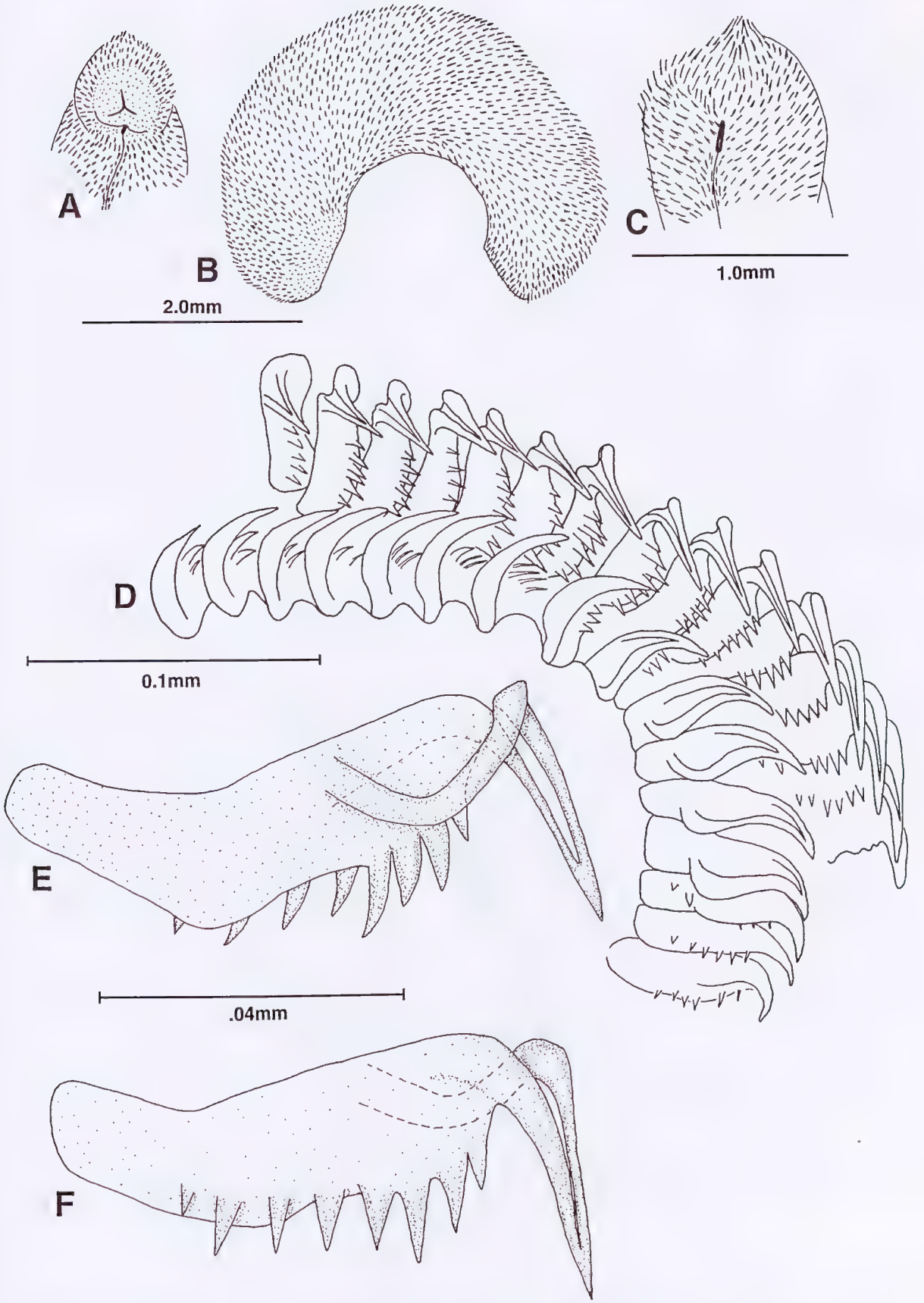

Figure 4. *Ocheyoherpia trachia* n.sp. A–C, holotype (AM C203646): A, anteroventral end with flattened mouth area stippled, dorsal carina evident. B, entire specimen, anterior to left. C, posteroventral end. D–F, radula of paratype (AM C203647): D, entire radula, distal end to left; one tooth missing, right row. E, single tooth viewed from beneath radular membrane showing supporting bar fused to lateralmost denticle. F, same tooth as if viewed from above.

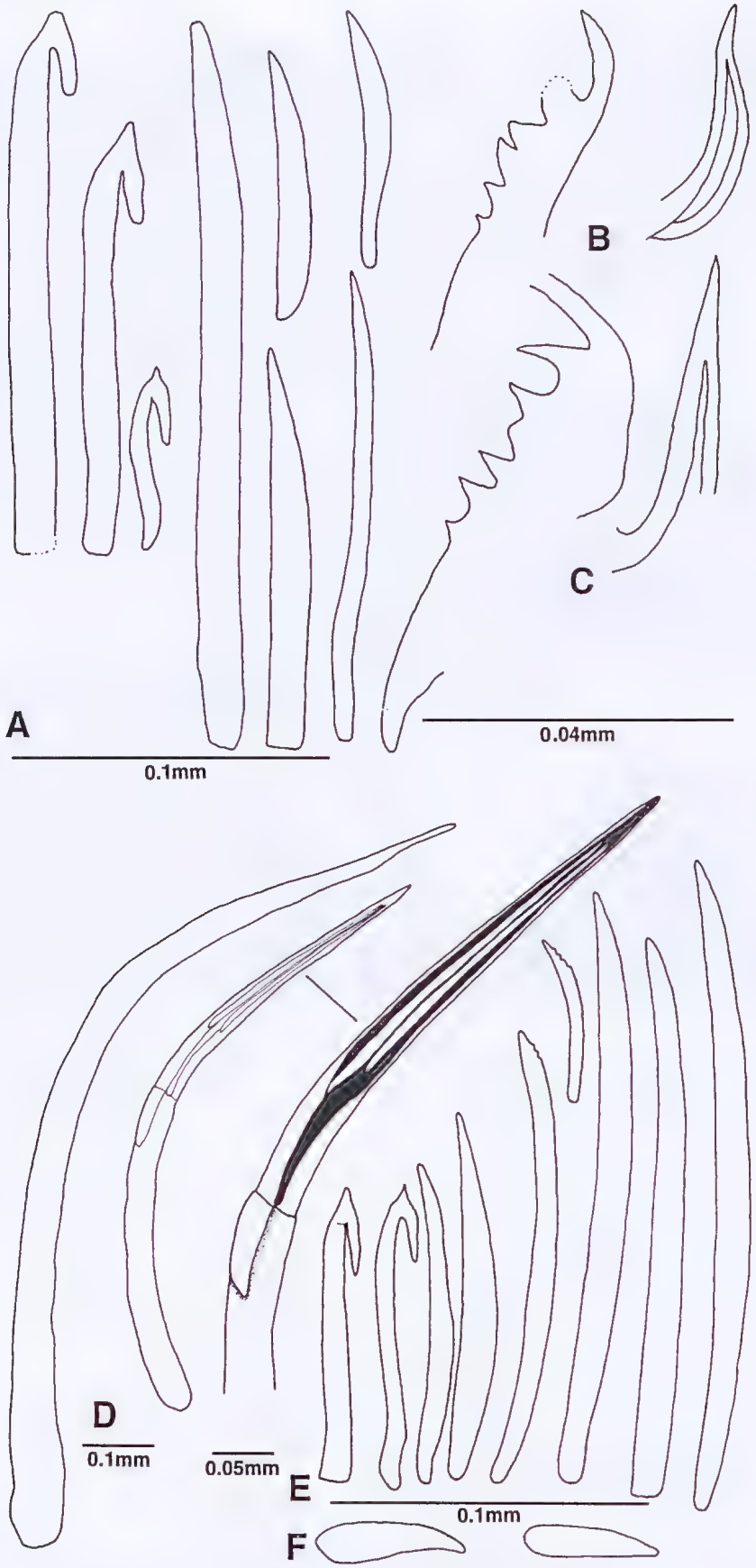

Figure 5. A, *Ocheyoherpia lituifera* Salvini-Plawen, epidermal spicules from holotype; spicules with distal serrations not illustrated. B, *O. lituifera*, radular teeth drawn from sectioned paratype, distal end of fused lateral denticle curved (USNM 749739). C, *Ocheyoherpia trachia* n.sp., radular teeth drawn from sectioned specimen (AM C149636) at same scale as B. D–F, *O. trachia* n.sp., spicules from paratype (AM C203647) except left barbed spicule from paratype (AM C203648); D, copulatory spicules; E, epidermal spicules; F, spicules from beside pedal groove.

Description. Spicular coat rough; anterior and posterior ends of body not tapered, flattened ventrally (Figs. 3E, 4B); with dorsal carina; retracted mouth slit an inverted Y-shape, opening of mantle cavity axial, short (Fig. 4A,C); body length to 6.5 mm, height even throughout, to 1.4 mm. Epidermis and cuticle thin, to 18 μm and 22 μm, respectively. Epidermal spicules evenly curved, to 210 μm long by 14 μm wide and more than 10 μm thick, bluntly pointed distally, base slightly tapered with end rounded to straight (Fig. 5E); serrated spicules few, from anterior body only, especially near mouth; few spicules with recurved base; barbed spicules to 128 μm long by 9 μm wide, not numerous; spicules from beside pedal groove nearly ovate but tapered and often curved proximally (Fig. 5F). Radula (3 examined) with about 16 rows of teeth (Fig. 4D); tooth base about 75 by 18 μm, medial one-third attached to radular membrane, number of denticles 7 to 9 excluding lateral fused denticles (Fig. 4E,F); radula ending distally in two lateral pouches of pharynx. Copulatory spicules (1 specimen examined) deeply curved, two per copulatory spicule sac, 1.3 mm and 0.9 mm long, curve nearly 90° (Fig. 5D); longer spicule simple, shorter spicule with ridges and processes on distal half.

Reproductive system. The reproductive system and copulatory apparatus follows that of *O. lituifera* (Salvini-Plawen, 1978, figs. 95, 96) with these exceptions: (*a*) There are paired, large seminal vesicles opening off the ducts leading from the gonads to the pericardium (gono-pericardioducts). (*b*) The paired copulatory glands, voluminous proximally and ending in narrow tubes as in *O. lituifera*, open into the grooved and ridged distal end of the ventral, smaller copulatory spicule shown in Fig. 5D and not into a triangular tube formed by 3 small copulatory spicules as in *O. lituifera*. (*c*) The copulatory spicules are deeply curved, not nearly straight as illustrated for *O. lituifera*. (*d*) One pair of copulatory spicules (the smaller?) opens into the mantle cavity on papillae (the sections were too poor in this area to ascertain where the second pair of copulatory spicules end).

Remarks. Besides the differences in the reproductive system noted above, *Ocheyoherpia trachia* differs from *O. lituifera* in being less spiny and in having a carina, a large dorsal sinus, a thinner cuticle, narrower and shorter epidermal spicules, fewer barbed spicules, and a larger radula (Fig. 5B,C).

ACKNOWLEDGMENTS. Type material was kindly loaned by the National Museum of Natural History, Washington, DC, and by Dr L. v. Salvini-Plawen. Much of the work was done under a PEET grant (Partnerships for Enhancing Expertise in Taxonomy) from the United States National Science Foundation DEB-9521930. Contribution no. 9745 from the Woods Hole Oceanographic Institution.

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Pilbarophreatoicus platyarthricus n.gen., n.sp. (Isopoda: Phreatoicidea: Amphisopodidae) from the Pilbara Region of Western Australia

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ABSTRACT. *Pilbarophreatoicus platyarthricus*, a subterranean phreatoicidean isopod from an intermittent stream in the arid Pilbara region of northwestern Western Australia, is described. With subterranean morphofacies, namely slender vermiform body, eyeless, anteroventral lobe on pereonite 1, reduced abdominal epimera, clearly demarcated pleotelson and lacking in pigment, the species is distinguished particularly by details of the pleotelson. *Pilbarophreatoicus platyarthricus* is a Gondwanan relic surviving in an aquifer in a region with marked surface aridity. Discovery of *P. platyarthricus* highlights the importance of groundwater as a reservoir of biological diversity.

KNOTT, BRENTON, & STUART A. HALSE, 1999. *Pilbarophreatoicus platyarthricus* n.gen., n.sp. (Isopoda: Phreatoicidea: Amphisopodidae) from the Pilbara region of Western Australia. *Records of the Australian Museum* 51(1): 33–42.

The Phreatoicidea are ancient isopods, constituting the earliest derived members (Brusca & Wilson, 1991) and having the longest known fossil record of all living isopods. Their fossil record dates from the Essex fossil beds at Mazon Creek, Illinois, USA, of the Upper Carboniferous (Schram, 1970). Pre-Triassic representatives are known from marine deposits in the Northern Hemisphere (Birstein, 1962; Glaessner & Malzhan, 1962) but their post-Triassic record is exclusively from fresh waters of several of the Gondwanan fragments (Australia, New Zealand and South Africa), with maximum species diversity and abundance in the Bassian zoogeographic province of southern Australia (Knott, 1975). Phreatoicidean diversity in northern, by comparison with that of southern, Australia seems much reduced with the only records, until recently, from the South Alligator River area of the Northern Territory (Nicholls, 1943; Knott, 1975). However, information about the groundwater fauna of north-western Australia is increasing and more phreatoicideans are being found. *Crenisopus acinifer*, from a freshwater spring in the Kimberley region of Western Australia, was described by Wilson & Keable (in press). In addition, Wilson & Ponder (1992) described two species of *Tainisopus* from a cave pool and a spring outflow in the Kimberley that resembled phreatoicoideans, although they were not assigned to a currently described isopod suborder or family.

Annual rainfall in southern Australian sites, on the South Alligator River and at Kimberley sites where phreatoicideans have been collected is comparatively high (600–1,000 mm). The discovery of a new phreatoicidean from an intermittent stream in the arid Pilbara region (annual rainfall <300 mm) is biogeographically significant. This paper provides a description of the new species, for which a new genus is described, and highlights the zoological importance of groundwater in arid areas.

Family AMPHISOPODIDAE Nicholls, 1943

Pilbarophreatoicus n.gen.

Type species. *Pilbarophreatoicus platyarthricus* n.sp. by monotypy

Diagnosis. Body slender, vermiform, smooth dorsally with scattered setae. Head longer than deep, with sub-antennary lobe lacking incisure on anterior margin; eyes absent; mandible placed anteriorly; cervical groove weakly developed. Pereonite 1 free from the head with anteroventral lobe prominent and overlapping head; pereonites 3 and 4 longest, pereonites 5–7 short but deeper than other pereonites; epimera of pleonites 1–5 short; pleotelson long, emarginate and not upturned, telsonic pleura broadly bilobed. Left and right mandibles with *lacinia mobilis*, gnathopod with oblique palm and two strong buttresses, mid-appendage articles (particularly the merus) of pereopods 2–4 broadly expanded; pleopods without epipodites. Uropods robust, distal corner of upper margins marked by stout simple seta and with simple seta below insertion of endopod and exopod, which both terminate in one robust seta; exopod rotated to lie below endopod.

Etymology. The generic name is derived from the Greek *phreatoic*, meaning well-dweller, and from Pilbara, referring to the geographical area where the specimens were collected. Gender: masculine.

Remarks. Hypogean phreatoicideans are known from all three extant families (Amphisopodidae, Nicholllsiidae, Phreatoicidae) (Nicholls, 1943, 1944; Tiwari, 1955). *Pilbarophreatoicus platyarthricus* clearly belongs to the lineage retaining a *lacinia mobilis* on both left and right mandibles (Amphisopodidae and Nicholllsiidae) but lacks elongate uropodal exopods and cleft pleopodal endopods, which are characteristic of males of species of Nicholllsiidae (recorded only from deep wells in a small area of the Gangetic Plain between Varanasi and Patna in India) (Tiwari, 1955). *Pilbarophreatoicus platyarthricus* is therefore assigned to the family Amphisopodidae.

Pilbarophreatoicus platyarthricus n.sp.

Figs. 1–6

Type material. HOLOTYPE: male, 12 mm, partially dissected with appendages on 2 slides, Western Australian Museum of Natural Science WAM C 23241, Nyeetberry Pool (21°51.6'S 116°30.7'E by GPS) on Jimmawurrada Creek, tributary of Robe River, Pilbara, 2 May 1995, W.R. Kay & M.R. Smith. PARATYPES: 2 juveniles, WAM C 23242, same location, 2 May 1995, W.R. Kay & M.R. Smith. 3 juveniles, WAM C 23243, same location, W.R Kay & M.R. Smith, 11 May 1996.

Additional material examined: 5 males (7.4–11.4 mm long), 10 females (5.7–7.7 mm), 2 juveniles (5.3, 5.7 mm), WAM C 24156, Chalyarn Pool, Robe River (21°45.2'S 116°02.1'E, ≈50 km E of Nyeetberry Pool), 18 April 1998, J.M. McRae. 1 male, 1 female, Australian Museum P 53154, Chalyarn Pool, 18 April 1998, J.M. McRae.

Description of holotype male. Body (Fig. 1) slender, attenuated with parallel sides, smooth with scattered short setules dorsally, particularly on the anterior margins of thoracomeres 2–5; lacking pigment in 70% ethanol.

Head longer than deep; cervical groove weakly developed; prominent sub-antennary lobe lacking incisure on anterior margin; ventral margin slightly concave along line of articulation with mandible and also over remaining mouthparts; eyeless.

Antenna 1 (Fig. 2) short, reaching to base of peduncle article 5 of antenna 2; with 7 articles, 1–4 decreasing in length, 5 just shorter than 1, 6 longest and widest, 7 shortest; aesthetascs single on articles 7 and 5, clumped on 6; plumose setae on articles 2 (predominantly) and 1, large seta on 3. Antenna 2 (Fig. 2) peduncle with 5 articles, 3–5 being particularly setose; flagellum of 21 articles, each bearing setae sub-terminally. Upper lip (Fig. 3) slightly asymmetrical. Both mandibles stout and with triturative molar process. Left mandible (Fig. 2) incisor process with 4 teeth; *lacinia mobilis* with 3 teeth; spine row of 5 denticulate and several simple spines; molar process with convex grinding surface, armed with 3 plumose setae and 1 simple seta; palp of 3 articles, 1 shortest, 2 (rectangular) and 3 (ensate) approximately equal in length along the midline; palp article 1 with 2 setae, 2 with 3 prominent bipectinate setae distolaterally and row of setae mesially, 3 with sub-apical plumose setae extending to apical brush of long setae. Right mandible (Fig. 2) incisor process with 4 robust teeth; *lacinia mobilis* well developed with 3 teeth; spine row with 8 denticulate setae; molar process prominent and with concave triturating surface; palp similar to that of left mandible. Lower lip (Fig. 3) bilobed, setae apically and mesially. Maxilla 1 (Fig. 3) endopod with 4 long and 1 short plumose apical setae, mesial margin lined with row of short setae; exopod with 13 stout teeth apically, lacking palp. Maxilla 2 (Fig. 3) exopod bilobed, each lobe armed apically with a row of long pectinate setae; endopod with two rows of long seto-spines, simple and pectinate, on apical and mesial margins. Maxilliped (Fig. 3) endopod long and narrow, with pectinate setae along the distolateral and apical margins;

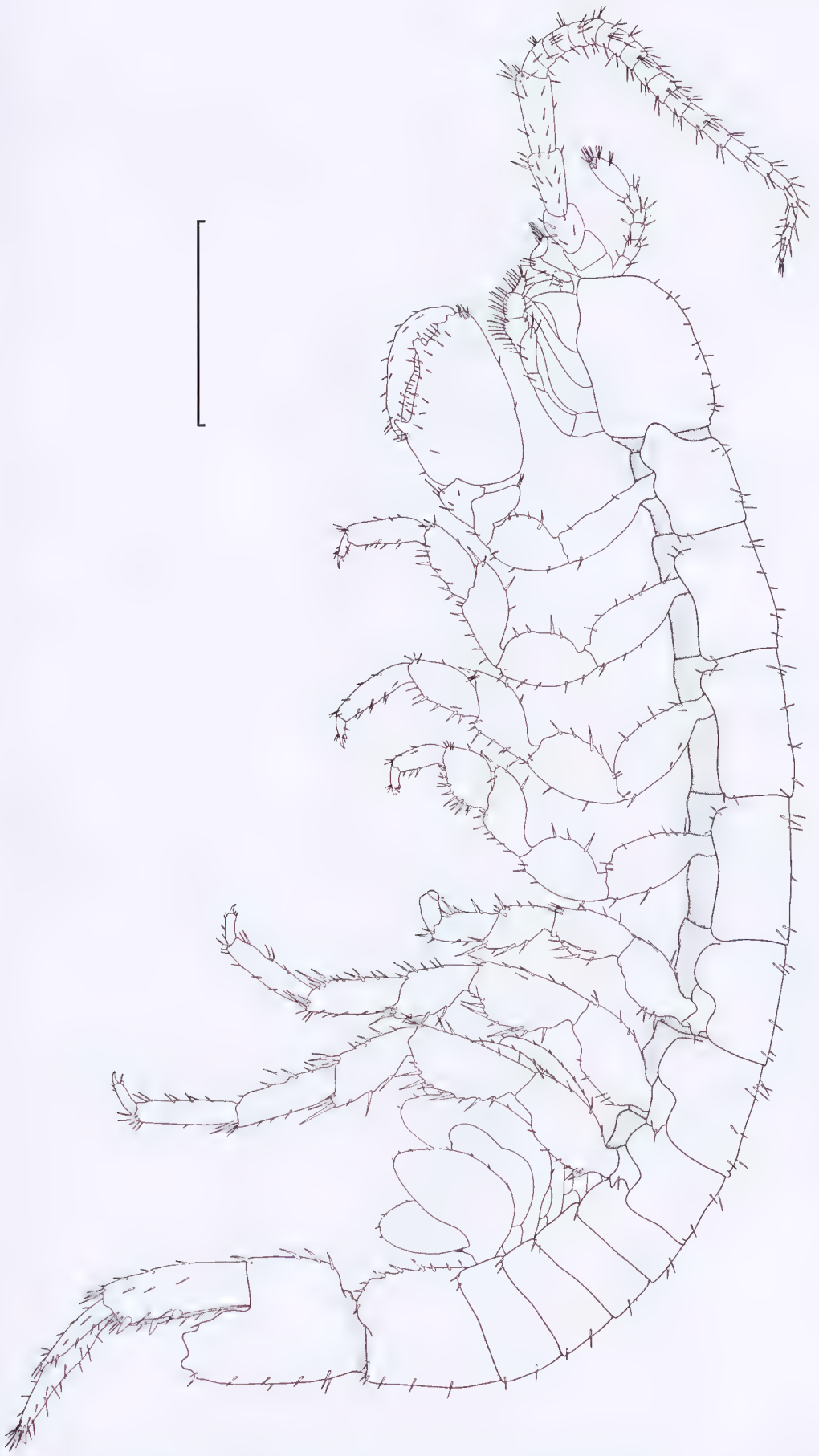

Figure 1. *Pilbarophreatoicus platyarthricus*, holotype male, lateral view, scale = 1 mm. Whole animal.

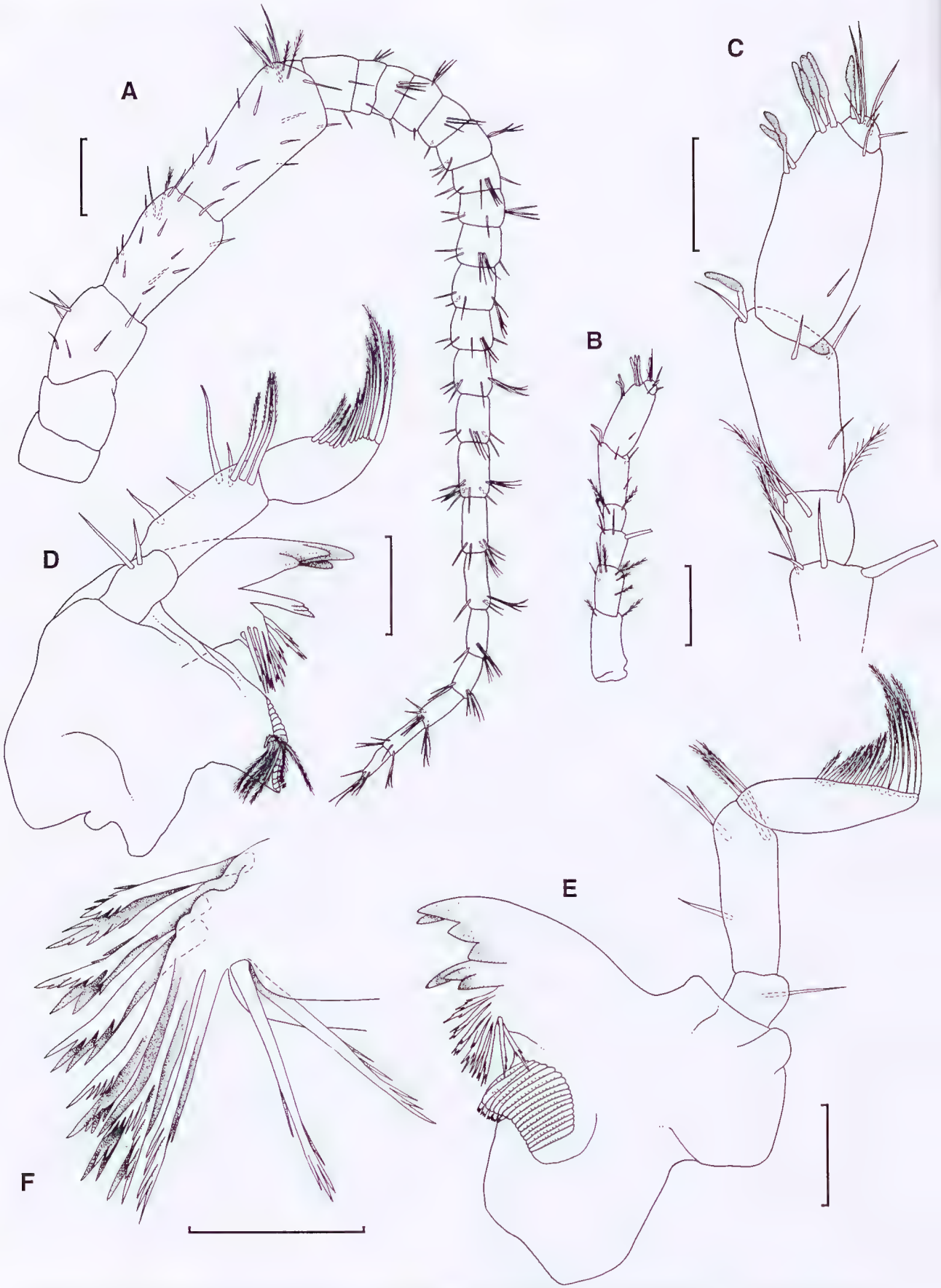

Figure 2. *Pilbarophreatoicus platyarthricus*, holotype male. A, left antenna 2. B, left antenna 1. C, detail of aesthetascs on antenna 1. D, left mandible. E, right mandible. F, spine row of right mandible. A, B scale = 0.2 mm, C–E scale = 0.1 mm; F scale = 0.05 mm.

Figure 3. *Pilbarophreatoicus platyarthricus*, holotype male. A, left maxilla 2, showing detail of two types of setae. B, upper lip. C, lower lip. D, ventral view of maxilliped. E, medial view of maxilliped with detail of seta. F, right maxilla 1. A–F scale = 0.1 mm; A, E enlargements scale = 0.02 mm.

palp of 5 articles, 1 short, 2 expanded laterally, 3 with prominent inner margin lined with row of long setae, 4 and 5 with marginal setae.

Pereonites 3 and 4 longest, 1 and 7 shortest. Tergites of all pereonites longer than deep; when depth to sternite is considered depth of pereonites 1, 6 and 7 just greater than length, length of pereonites 2–5 greater than depth. Pereonite 1, free from head, anterior margin of tergite expanded ventrally into pronounced lobe overlapping head. Ventral margins of pereonites 2–4 slightly concave between small lobes at anterior and posterior corners of each body segment; pereonites 5–7, convex anteriorly and strongly concave along junction with coxa. Sternites of pereonites 5–7 with prominent midventral protuberance. Coxae 1–4 are inserted anteriorly on pereonite, coxae 5–7 are inserted on posterior half of the respective pereonite. Coxae 1–4 immovable, 5–7 movable with a seta on the posterior lobe.

Gnathopod (Fig. 4) with basis not expanded, ischium expanded anteriorly, merus expanded anteriorly and buttressing against enlarged propodus, carpus small and articulating with the posterior margin of propodus; propodus longer than wide with an oblique, crenulated palm delineated distally by prominent buttress and proximally by a large spur; on each side of palm are two rows of setae, dactylus has dagger-shaped terminal section carrying 2 setae. Pereopods 2 and 3 (Fig. 4) similar, ischium expanded anteriorly, merus with prominent anterodistal expansion, dactylus bearing secondary unguis. Pereopod 4 (Fig. 4) with broadened carpus with row of spines on posterior margin, dactylus with 2 pegs. Pereopods 5 and 6 (Fig. 4) with anterior margin of basis curved convexly, posterior margin expanded proximally through convex curve and narrowing distally through concave curve; ischium broadly triangular with posterior expansion. Pereopod 7 longest. Margins of all articles, particularly of pereopods 2–7, armed with stout setae. Penis broad, rectangular, unarmed, attached at the coxa/sternite junction; both penes meeting in the midline of the body.

Pleonites 1–6 increasing slightly in depth (Fig. 1). Pleonite 5 is >2 × length of each of pleonites 1–4. Epimera short, covering pleopod peduncles; posteroventral lobes bearing 1 or 2 setae; posteroventral lobe and ventral margin of epimeron of pleonite 5 with row of setae. Pleotelson with anterior waist; ventro-lateral margin with 3 marginal and 2 submarginal setae; posteriorly, lateral margins bilobed, dorsal lobe bigger than ventral; posterodorsal margin produced into broad, short pleotelson, which is shallowly and asymmetrically cleft and turned downwards, with several fine setae on margin of cleft. Anus lies at base of tube formed from the pleotelson dorsally and ventrally by a cuticular ridge (Fig. 5).

Pleopods (Fig. 6) biramous with length decreasing from 1 to 5; peduncles arranged nearly transverse to main body axis with mesodistal corner rotated posteriorly. Exopod of pleopod 1 simple, pleopods 2–4 with medial lobe. *Appendix masculinis* of pleopod 2 short and curved, reaching just beyond edge of endopod. Uropod (Fig. 5) peduncle with 3 small setae ventrally, both upper margins lined with setae and large robust seta at distal corner (outer, submarginally); 1 simple seta and several setae ventrally below the insertion of the rami; exopod 2/3 length of endopod, rotated to lie ventral to endopod, which has lateral subterminal setal tuft and terminates in movable seta.

Females. Oostegites on pereonites 1–4 inclusive; differs from male in gnathopod—propodus markedly triangular and palm lacking spine and buttress but with long setae on the lobe; carpal lobe of pereopod 4 lobe not pronounced, spine row less distinct; sternite of only pereonite 7 is prominently ridged; pleopods similar in length.

Juveniles carry same-shaped gnathopods as females.

Etymology. The name *platyarthricus* is derived from the Greek meaning broad articles, referring to the expanded articles, particularly the merus, of several pereopods.

Remarks. Some character variation is evident among specimens from Nyeetberry Pool. For example, in males, number of articles in the flagellum of antenna 2 varies between 18 and 30, and in the 2 specimens with both flagella intact, number on either side differs. Setation is more pronounced in larger specimens, with an anterior line of short setae across each pereonite. Numbers of setae on limb articles and tergites is variable.

Pilbarophreatoicus platyarthricus is distinguished from other Australian groundwater isopods within the genera *Hyperoedesipus*, *Hypsimetopus* and *Phreatoicoides* by robust antennae 1 and 2, two prominent spurs on buttresses on the palm of the gnathopod, degree of expansion of ischium and merus (in *Phreatoicoides* only merus is expanded) and, particularly, in details of the pleotelson, which is emarginate (truncated in *Hypsimetopus*) with anus at base of a well defined tube (in other phreatoicideans anus is positioned close to the level of the body surface), broadly bilobed posterolateral margin, and uropod endopods and exopods terminating in movable setae (in *Hyperoedesipus* there is an indication of a terminal seta but it is immovable).

Groundwater phreatoicideans have few characters that indicate relatedness to surface dwelling forms, although Knott (1975) found the condition of the gut, whether with typhlosole and/or gut caecae, to be a reliable indicator of subfamily (*sensu* Nicholls, 1943, 1944) relationships. The faecal strand in the anus of *P. platyarthricus* is round, indicating an alimentary tract lacking a typhlosole; the specimen was not dissected to observe the gut caecae. Members of the Mesamphisopodinae and Amphisopodinae lack a typhlosole and hind gut caecae, whereas at least some representatives of the Hypsimetopinae from southeastern Australia have a typhlosole and numerous, small hind gut caecae. Given the present distribution of the subfamilies Mesamphisopodinae (South Africa, Northern Territory and southern Western Australia) and Amphisopodinae (southern Western Australia and mound springs near Lake Eyre, South Australia), *P. platyarthricus* appears to represent a subterranean invasion of ancestors originally spread across the African/Western Australian region of Gondwana.

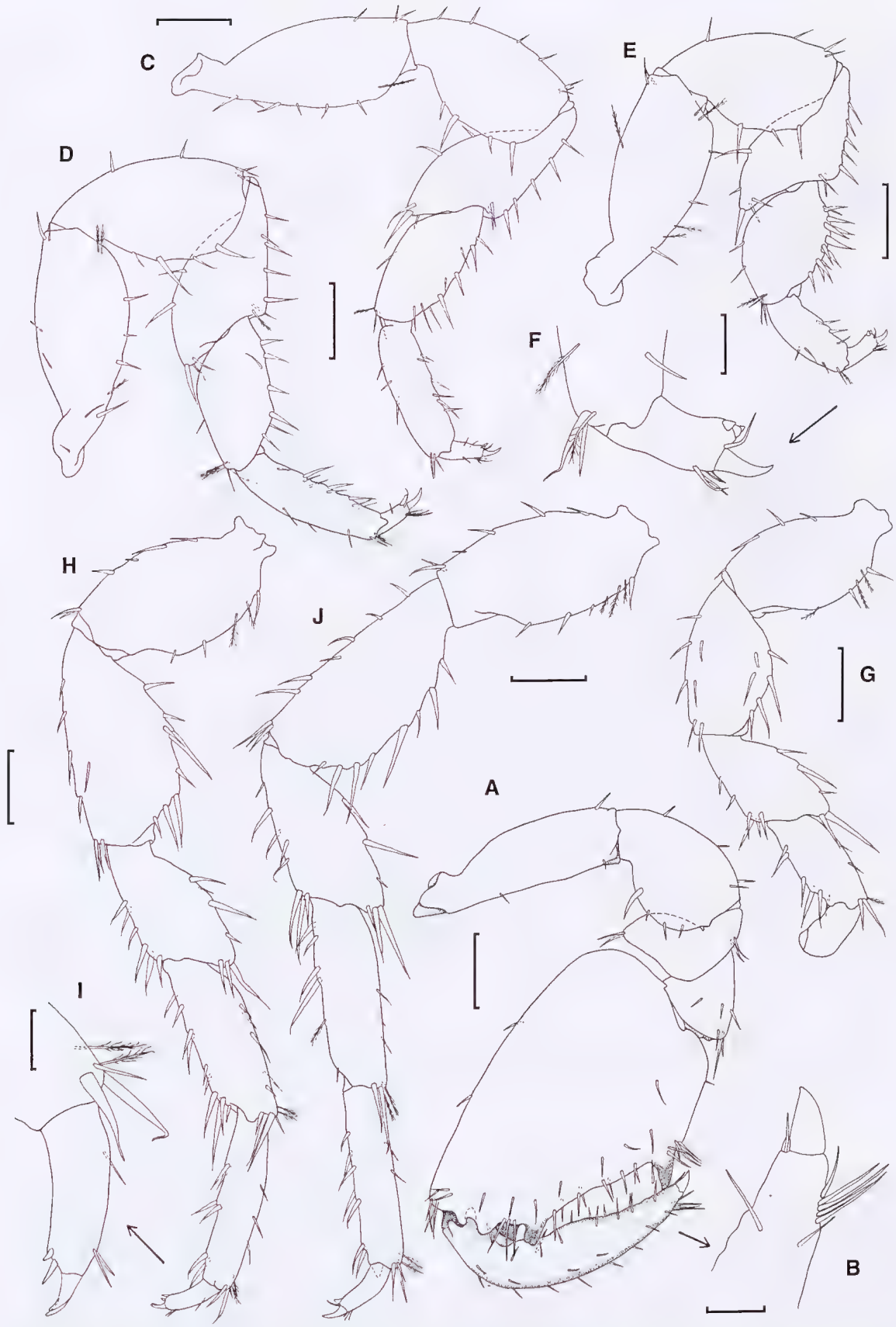

Figure 4. *Pilbarophreatoicus platyarthricus*, holotype male. A, right gnathopod. B, detail of dactylus of right gnathopod. C, right pereopod 2. D, right pereopod 3. E, right pereopod 4. F, detail of dactylus and unguis of right pereopod 4. G, right pereopod 5, dactylus and unguis regenerating. H, right pereopod 6. I, detail of dactylus and unguis of right pereopod 6. J, right pereopod 7. A, C–E, G, H, J scale = 0.2 mm; B, F, I scale = 0.05 mm.

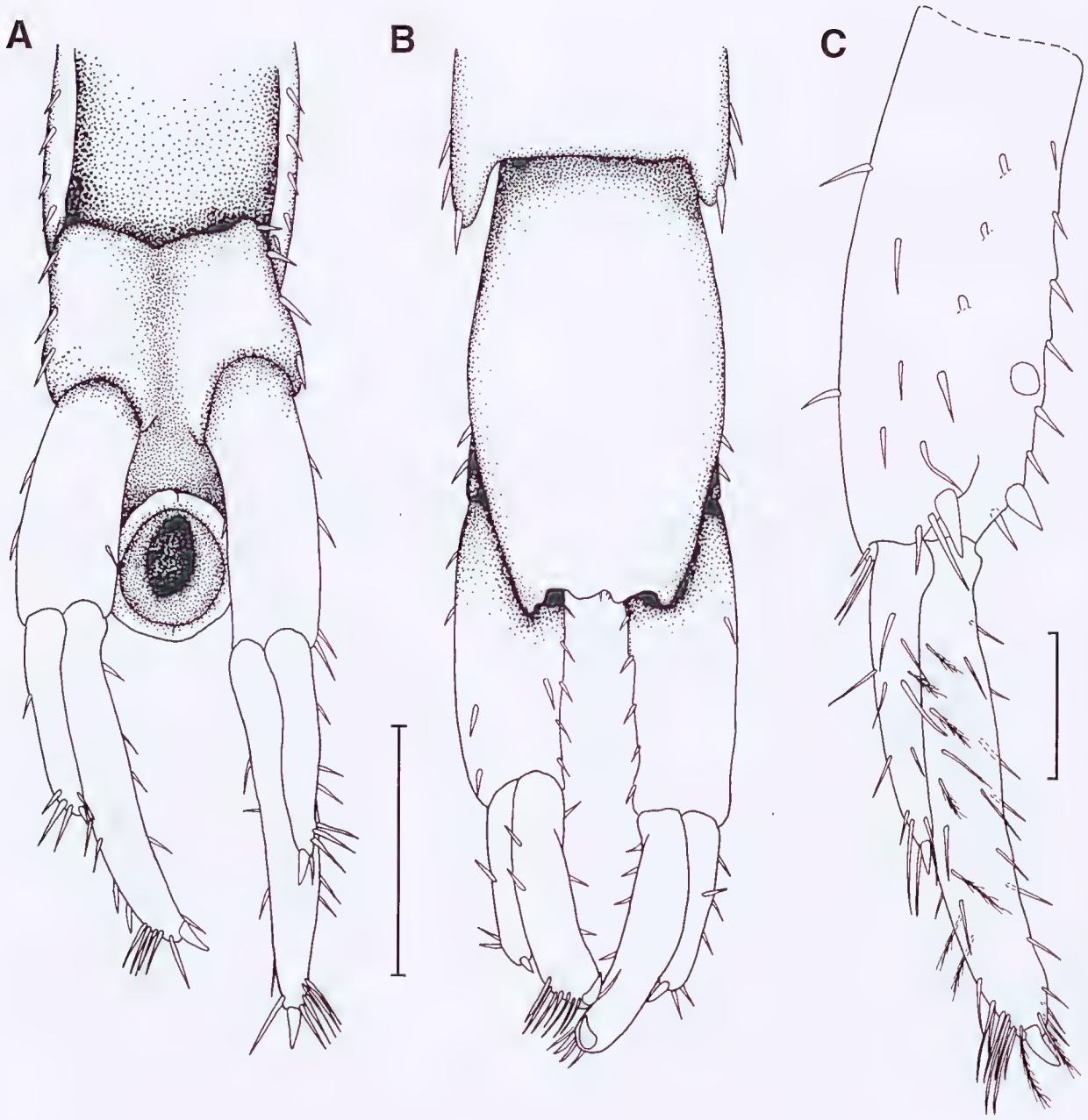

Figure 5. *Pilbarophreatoicus platyarthricus*, holotype male. A, pleotelson and uropods, ventral view. B, dorsal view. C, detail of right uropod, lateral view. A, B scale = 0.5 mm; C scale = 0.2 mm.

Discussion

Pilbarophreatoicus platyarthricus was collected from part of the Pilbara with median annual rainfall of about 300 mm and maximum temperatures often exceeding 45°C. All specimens were collected during the wet season (summer/autumn) from under cobbles in slow-flowing riffles in small pools of permanent water, maintained by groundwater discharge, on the Robe River. Other sections of the river, like streams elsewhere in the Pilbara, dry between periods of flow. Water in Nyeetberry Pool was fresh (780 µS/cm in 1995, 675 µS/cm in 1996) with alkalinities of 330–320 mg/L and pH values of 7.8–7.6. Water in Chalyarn Pool was also fresh (1144 µS/cm) with pH 7.6 in 1998. Most subterranean phreatoicideans in southern Western Australia occur in freshwater of similar, or slightly higher, salinity (B. Knott, unpublished data).

This is the first account of a phreatoicidean from the Pilbara region of Western Australia. The species was not found during the dry season when, presumably, animals had retreated deeper in the riverbed. The slender vermiform body, lack of eyes and pigment, reduced abdominal epimera, and anteroventral lobe on pereonite 1 are typical of hypogean phreatoicideans (Knott, 1975) and provide

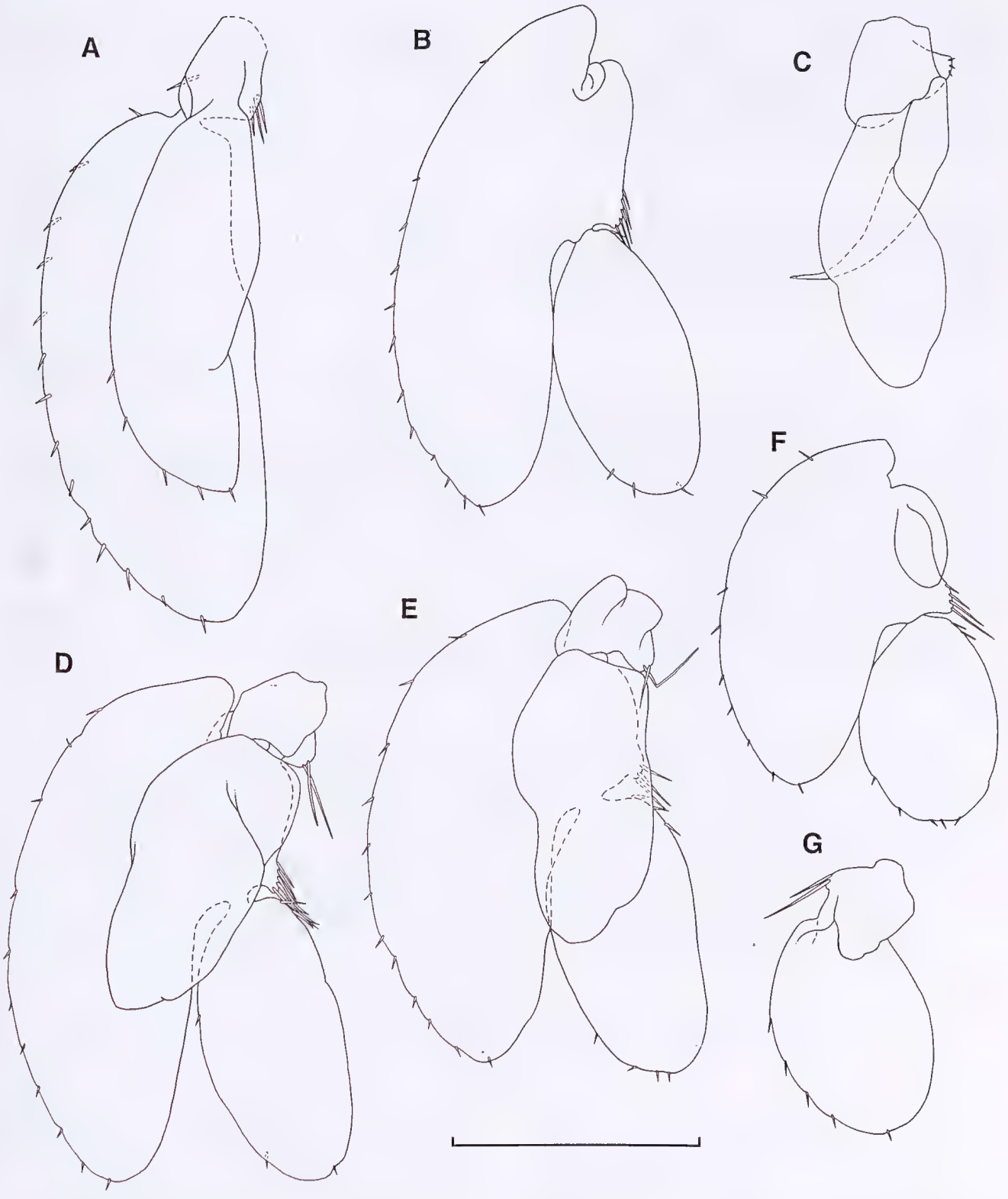

Figure 6. *Pilbarophreatoicus platyarthricus*, holotype male. A, right pleopod 1. B, exopod of right pleopod 2. C, endopod of right pleopod 2 with *appendix masculinis*. D, right pleopod 3. E, right pleopod 4. F, exopod of right pleopod 5. G, endopod of right pleopod 5. A–G scale = 0.5 mm.

morphological evidence, in addition to the habitat data, that *Pilbarophreatoicus platyarthricus* lives in groundwater. Its hypogean habits enable survival in an arid environment where surface water may occasionally dry out even in the deepest groundwater-fed pools.

Other relict, ancient freshwater crustaceans have also been recorded from the extensive groundwater reservoirs of the Pilbara (Poore & Humphreys, 1998), which seems to be a region of particular biogeographic importance, although its aquatic fauna is poorly known. Karst systems (Poore &

Humphreys, 1998), peat accumulations associated with outflow points of palaeorivers now flowing predominantly underground (Wyrwoll *et al.*, 1986), and groundwater discharge sites in modern rivers (Kay *et al.*, 1999) are likely to harbour phreatoicideans which, if their pattern of diversity elsewhere is a reliable guide, are likely to represent monotypic genera, each with limited distribution.

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Waite's Blind Snakes (Squamata: Scolecophidia: Typhlopidae): Identification of Sources and Correction of Errors

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ABSTRACT. The majority of the 542 typhlopid specimens examined by Edgar Waite for his 1918 monograph of the family are identified, and their current status discussed. Most Waite records that do not correspond with the distribution based on modern records are shown to be in error, involving either misidentifications, misreadings of localities, or transposition of data. A few remaining problematic records are considered dubious due to a lack of supporting data.

Ramphotyphlops batillus (Waite, 1894), known only from the holotype from Wagga Wagga, NSW, is restored to the Australian fauna, and new data on the type are provided.

Probable paratypes for *Typhlops grypus* (SAM R849; QM J2947), *T. proximus* (AM R615, R145401–07, SAM R915) and *T. subocularis* (AM R2169) are identified. New data on dorsal scale counts are provided for *Ramphotyphlops leucoproctus* (377–394), *R. polygrammicus* (370–422), *R. proximus* (326–392), *R. wiedii* (381–439) and *R. yirrikalae* (447–450).

SHEA, GLENN M., 1999. Waite's blind snakes (Squamata: Scolecophidia: Typhlopidae): identification of sources and correction of errors. *Records of the Australian Museum* 51(1): 43–56.

Although a number of species of Australian typhlopid snakes had been described by European herpetologists in the nineteenth century, notably Wilhelm Peters and George Boulenger, it was the publications of Edgar Ravenswood Waite (Waite, 1893, 1894, 1897a,b, 1898, 1917, 1918a), culminating in a revision of the family in Australia (Waite, 1918b), that provided the basis of knowledge of the Australian typhlopid fauna. In the 80 years since Waite's final revision, despite several new species being described (Parker, 1931; Kinghorn, 1929a, 1942; Loveridge, 1945; Robb, 1972; Storr, 1983, 1984; Ingram & Covacevich, 1993; Aplin & Donnellan, 1993; Shea & Horner, 1997; Aplin, 1998; Couper *et al.*, 1998) only one significant revision of Australian typhlopids has appeared (Storr, 1981). Waite's work, particularly his key, distribution maps and figures, has been the main source of much of the subsequent literature on Australian typhlopids.

Waite's typhlopid work set new standards for Australian herpetology by attempting to use all available material, not just the specimens available in a single institution. Despite this use of large amounts of material from diverse sources to derive his distribution maps, he provided precise locality data for few specimens, and cited museum numbers only for primary type specimens he had described. Many of the species were known from only a few specimens, from widely separated localities. Distribution maps and statements derived from these initial mapping efforts have often joined these widely-spaced sites to produce broad,

almost Australia-wide distributions for many species (Kinghorn, 1929b, 1956; Worrell, 1963; Cogger, 1975; Wilson & Knowles, 1988; Gow, 1989; Hoser, 1989; Mirtschin & Davis, 1992) that have not been supported by subsequent workers using modern material (Storr, 1981; Swan, 1990; Ingram & Raven, 1991; Ingram & Covacevich, 1993; Shea, 1995; Shea & Horner, 1997).

This paper is the result of a search of early Australian museum collections and registers to attempt to identify the basis for Waite's typhlopid distribution records, particularly those that are well outside distributions as currently known, with the aim of reconciling these anomalies. In the course of this work, new data on morphological variation became available for several poorly-known species, and are presented herein.

Waite (1918b: 1) reported examining 542 specimens in the following collections: the Australian Museum, Sydney; Macleay Museum, Sydney; National Museum of Victoria, Melbourne; Queensland Museum, Brisbane; South Australian Museum, Adelaide, and Western Australian Museum, Perth. The status of pre-1918 collections in each institution is documented below, for the purposes of identifying the material available to Waite.

1. Australian Museum (AM). Registration of the herpetological collections in the Australian Museum began about 1877, with a specific herpetology register beginning in 1886 (Cogger, 1979; Shea & Sadlier, 1999). Waite arrived in Australia in 1892 to take up a post at the Australian Museum. He resigned from this position in March 1906 to go to the Canterbury Museum in New Zealand, and in April 1914 became Director of the South Australian Museum (Cogger, 1979; Hale, 1928; Jones, 1992, 1995; Tyler & Hutchinson, 1993). Waite's early work on typhlopids was undertaken during his tenure at the Australian Museum, and seems to be largely based on Australian Museum material (Waite, 1893). Large numbers of typhlopids were registered during the period of Waite's employment, and he actively solicited material (Waite, 1893).

Many typhlopid records in the Australian Museum registers are stamped in blue ink "identified by Waite 1918", and these stamped entries end with a number of previously unregistered typhlopids registered as a block (R6554–88) in January, 1914. However, these identifications do not include all the typhlopids examined by Waite, as there are a number of specimens not so identified which uniquely fit localities given by Waite (1918b). Only two typhlopids were registered between R6588 and the end of 1918. Neither can be unequivocally identified as examined by Waite, although one AM R6716, *R. ligatus* (Lightning Ridge) does not correspond to a map locality (but see comments below, under *ligatus*). Hence, it is assumed that R6588 marks the end of the typhlopids available to Waite.

Determination of which pre-1918 typhlopids were identified by Waite is difficult because a number of specimens were exchanged with other institutions prior to 1918, and a number of specimens were destroyed in February 1914 due to poor condition. A large collection was exchanged to the Museum of Comparative Zoology in 1914, where they were reported on by Loveridge (1934). Some of these were registered pre-1906, and would have been available to Waite while he was at the Australian Museum. However, none of the unique localities associated with these specimens correspond to map localities from Waite (1918b), and I assume that Waite's maps are derived only from specimens examined subsequent to his return to Australia. Even with the removal of these records, there are a number of specimens that cannot be confirmed as examined by Waite, as they have imprecise locality data which would not have been mapped, or come from regions well represented in collections, where one dot on a map would suffice for a number of specimens.

2. Macleay Museum (MM). The Macleay Museum at the University of Sydney has had a chequered history. The basis for the collection is the private collections gathered by three members of the Macleay family, particularly William John Macleay. The "Macleayan Collection" was donated to the University of Sydney in 1890, just before W.J. Macleay's death in 1891, with the requirement that it be curated by Macleay's curator, George Masters. Following Masters' death in 1912, the collection was poorly maintained for over fifty years, and a number of specimens were damaged, destroyed or lost associated data (Stanbury & Holland, 1988; Horning, 1994). No registration of herpetological specimens was undertaken until S.J. Copland began a personal registration system of numbers tied to specimens in the 1940s (Copland, 1946). In 1965, the curator of the Macleay Museum, Ms Jenny Anderson, began a register with a new system of numbering for all specimens in the herpetological collections (Goldman *et al.*, 1969). Thus some, but not all, specimens in the collection have two numbers, a formal registration number and a Copland number. Prior to registration, data for specimens was in the form of loose labels in or on the bottles containing specimens, and these labels have generally been retained with the specimens.

Waite studied the Macleay Museum collection in 1893 (Waite, 1893) and described one species from it in the following year (Waite, 1894), during his time in Sydney. Hand-written paper labels in most typhlopid bottles give identifications with Waite's initials in pencil, indicating his examination of these specimens. A few other bottles, although lacking these initialed labels, have similar labels with numbers up to 18, and probably represent the material loaned to Waite. The few typhlopids which lack both labels either lack all data, or are identifiable as later additions to the collection.

Curiously, although several typhlopids come from localities (King Sound, Darnley I., Cape Grenville) for which Macleay reported reptile collections (Macleay, 1877, 1888), he did not mention typhlopids in these papers.

3. Museum of Victoria (MV). Three systems of registration have been employed for the herpetological collections at the Museum of Victoria (J. Coventry, pers. comm.). Early specimens were identified by unprefixed numbers in a system employed for the entire museum collection that probably commenced in 1854, and was used until about 1940. A second system with R-prefix, for all vertebrate specimens, began in the early part of the twentieth century,

prior to the present D-prefixed herpetological registration system, which commenced in 1933. Many of the early unprefixed and some of the R-prefixed numbers have been reregistered into the modern system. Waite did not report receiving typhlopids from the Museum of Victoria during his period in Sydney, although he did communicate with Frederick McCoy, the director, concerning typhlopids at this time (Waite, 1893). It is probable that he first received the Museum of Victoria typhlopid collections for study at the South Australian Museum following his return to Australia in 1914. A list of the MV specimens sent to Waite, together with his identifications of them, is contained in correspondence from Waite to Museum of Victoria dated 14.v.1918 (Coventry, 1970). The specimens examined fall into three series: R3080–81 (two specimens), R7055–147 (90 specimens) and R7165–204 (37 specimens). Dating these specimens is difficult. A column of dates in the register appears to be dates of receipt of the specimens, based on their arrangement. Not all specimens have dates, and the dates available are not in order, but grouped by collector or donor, regardless of locality. Thus, the date 1.viii.1908 is used for the series R7172–204, all received from the Western Australian Museum, with a range of localities, some localities with a second date, between 1896 and 1898. The latest date of receipt associated with these series is 26.iii.1917, for R7067, suggesting that the specimens were registered in 1917, probably as a block just prior to sending them to Waite.

4. Queensland Museum (QM). A separate register for the Queensland Museum herpetological collections did not commence until 1911, prior to which a complex system of separate donor, accession, purchase, exchange and collection registers was used for the entire museum collection (Covacevich, 1971). Waite reported examining the entire typhlopid collection between 1893 and 1894 (Waite, 1893, 1894), describing a new species from the material. He subsequently examined material registered post-1911, many of the registration entries in the modern system noting that the specimen was identified by Waite. Registration numbers were not consistently available for the early material, which was slowly incorporated into the modern system, some material being incorporated as recently as 1970 (Covacevich, 1971). Hence, it is not possible to fully identify the Queensland Museum material examined by Waite on the basis of registration data. However, as the material was loaned to Waite, it can be assumed that it would have been registered prior to sending it. Hence, typhlopids registered pre-1918 are likely to have been examined by Waite. The typhlopids registered pre-1918 include a large block of consecutively numbered specimens (J2935–54) from a variety of sources, registered between 29.v–2.vi.1917 and definitely including material seen by Waite on the basis of unique localities. The next typhlopid entries are a block of three specimens, J3004–06, registered 4.viii.1917, two of which are annotated as examined by Waite, and the last one of which also uniquely fits a Waite record. Then follow six typhlopids registered on three occasions between 6.ix.1917 and 22.iii.1918, none of which are annotated as examined by Waite, and for which the few localities do not correspond to Waite's maps. Hence, it is assumed that J3006 is the most recent specimen seen by Waite. It seems that not all typhlopids registered prior to this specimen were sent to Waite, as there are several unique records which do not appear in Waite's monograph. Further, only some typhlopid entries, even among series, are annotated as examined by Waite. Conversely, such annotations are not made for all specimens seen by Waite, as a few unique records corresponding to Waite's monograph are not so annotated.

5. South Australian Museum (SAM). On Waite's return to Australia from New Zealand in 1914, he became Director of the South Australian Museum. It seems his interest in Australian typhlopids was rekindled on his return with access to an extensive new collection (Waite, 1918b: 1). His 1918 typhlopid monograph was the first paper in the new "Records of the South Australian Museum", which he had initiated (Jones, 1995), and may have been hastily prepared to meet publication deadlines. Permission for the publication of the new journal was given on 18 September, 1917, and in the nine months before the publication of the first issue on 24 June 1918, he was heavily involved in planning the new publication in addition to his usual administrative work. In the final six weeks before publication, he was also planning for an expedition to New Guinea, leaving on the day of publication of the journal (Jones, 1995).

Registration of South Australian Museum herpetology collections began in 1911, with a large backlog of typhlopid material registered as a block (R802–R862) on 11.i.1918, probably indicating the completion of registration of material used for his monograph. A second block of typhlopids (R914–927) was registered on 3.x.1918, after the publication of his monograph, and consists of material received in exchange or by donation from other museums, and known to have been used by Waite in his monograph, together with some "old collection" specimens that do not correspond to localities in his monograph, and were presumably located after completion of the work.

6. Western Australian Museum (WAM). Although the Western Australian Museum was founded in 1892, registration of herpetological collections did not begin until 1912. Waite did not report examining material from the Western Australian Museum in his early papers, and probably borrowed the typhlopid collections to examine in Adelaide on his return to Australia. Early typhlopid registrations in this system, up to R630, registered May 1917, are mostly annotated as seen by Waite (either "identified" or previous identification "confirmed"). The few exceptions are generally either annotated "useless", and represent specimens disposed of at the time of registration, or do not correspond to Waite's localities, and hence were probably found in the collection after the loan was sent to Waite.

Waite's typhlopid records

For the purposes of conformity to Waite's papers, the species are listed as in their original combinations, although all Australian species are now placed in the genus *Ramphotyphlops* (Robb, 1966). In addition to the acronyms given above for Australian museum collections, the following acronyms are used: AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CAS, Californian Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard; NHRM, Naturhistoriska Riksmuseet, Stockholm; PNM, Philippine National Museum, Manila.

Dorsal scale counts are along the dorsal median scale row, from the first scale caudal to the rostral, to the scale immediately cranial to the terminal spine.

Typhlops affinis: Waite (1918b) reported examining only three specimens. One of these was from north Queensland, one from Eidsvold, and one from Campbelltown. The latter two localities are mapped, together with a literature record from Lönnberg & Andersson (1913) from Mallallah in the Kimberley. Modern records indicate a distribution only from central Queensland (Ingram & Raven, 1991) south to central-north NSW (the only definite NSW records being AM R16759, Mungindi; R135419, 6.5km NE "Karalee", NE of Enngonia, and R142984, 9km E "Beulah") in semi-arid habitats.

The Mallallah record is based on NHRM 2398, here reidentified as *R. grypus*. The specimen has 647 dorsal scales, dark head and tail, a hooked snout and the nasal cleft from the second supralabial. The Campbelltown record is probably based on AM R2422, a specimen of *R. affinis* with no locality, but with the previous registration number given the locality Campbelltown.

The only Waite localities supported by modern records are Eidsvold and north Queensland. Three early specimens correspond to the former record: AM R5333, R6343a–b (all from Eidsvold, donated T.L. Bancroft). The latter two specimens are identified in pencil in the original register as "nr *wiedii*, 18 scales, nasal cleft not on snout", suggesting uncertainty about their identification, and hence R5333 is probably the basis for the Eidsvold record. Waite's north Queensland specimen is MV R7055. One additional specimen of this species, AM R2722 (no locality) is recorded as identified by Waite in the registers, while another early AM specimen, R153041 (formerly 6426) (Gayndah) may have been overlooked by Waite.

Typhlops australis: Waite (1918b) maps two localities in the Northern Territory, well beyond the otherwise nearly continuous distribution in southern Australia. These are probably based on two "central Australian" localities listed by Waite: Fraser Range and McMinn's Creek. However, Fraser Range is in Western Australia, this record being based on AM R6583 (Fraser Range; Elder Expedition), the specimen identified as *Typhlops* sp. by Stirling & Zeitz (1893). The identification of this specimen is confirmed as *R. australis*. The McMinn's Ck locality is based on SAM R805 (McMinn's Ck, McDonnell Ranges, don. Illamurta Police Station), originally identified as *T. australis*, but which is now identified as *R. endoterus* (M. Hutchinson, pers. comm.).

Waite's map also has a locality for *R. australis* north of the Kalgoorlie area, well beyond recent records from Western Australia. This corresponds with a specimen, AM R3375, from Laverton (H.P. Richards). This juvenile specimen is confirmed as *R. australis*, and has 308 dorsal scales.

The third significant outlying locality on Waite's map is his only record for NSW, a dot in the vicinity of Wagga Wagga. However, a single specimen (AM R1197, Narrandera, J.A. Morris) was in the Australian Museum collection during Waite's period in Sydney, and the dot may be misplaced on the map.

Other map localities, within the known modern range (Storr, 1981; White, 1981; Swan, 1990; Coventry & Robertson, 1991), correspond to the following early records. From the Western Australian Goldfields, the three dots correspond to AM R3365, Boulder, AM R2172, SAM R172, Kalgoorlie and QM J119 (ex AM), J2951, Coolgardie, with an additional poorly localised specimen, WAM R27 (Goldfields), known to have been seen by Waite.

The five south-western Western Australian dots on Waite's map correspond to the following specimens of *R. australis*, of which the MV, SAM and WAM specimens were identified as such by Waite: AM R2372 (destroyed 1965), R2440–41, Perth; AM R2985, Harvey agricultural area, 80 mi. S Perth; MV R7181, Chidlow's Well; R7188–89, Mortlock, Perth (1898); R7191, Mandurah (1897); R7194, Perth (1898) (the latter five specimens received from WAM, presumably prior to the initiation of the modern registration system); SAM R859, Bunbury; WAM R212, Meckering; R456, Muchea and R620, Beechboro, with the Perth, Chidlow's Well, Mortlock, Mandurah and Beechboro specimens represented by a single dot (Waite, 1918b: 14). Additional specimens of *R. australis* available to Waite from this region were identified by him as *R. wiedii* (see below).

It has been possible to match specimens to most of Waite's South Australian localities, but not to all. The exceptions are among a number of dots along the coastal plain north of Adelaide, and two dots close to the Victorian border. Specimens which match mapped localities (including Adelaide suburban localities represented by a single dot; Waite, 1918b: 14) are: AM R131183 (formerly 6425), SAM R813, Pt Lincoln; MV R7063, Franklin Harbour; SAM R9, Tanunda and Murray Flats; R63, Salisbury; R281a–b, Eden Hills; R286, R439, Purnong; R299, Sleeps Hill; R393, Quorn; R411, Mulgundawa; R436, Mitcham; R478, Renmark; R480, Cleve; R627, Monarto South; R774, Wirrabara; R782, Angaston; R788, Loxton (now missing); R790, Karoonda; R806, Athelstone; R807, Orroroo; R808, Kapunda; R809, Emu Flat; R810, Lyndoch Valley; R812a–b, Stony Ck, Willowie Forest; R814, Nuccaleena; R815, Kapunda (now missing); R816, Laura; R817, Denial Bay; R818, Tea Tree Gully; R819, Edithburg (now missing); R820, Cowell; R821, Stockport; R822, Highbury; R825, Tanunda (now missing); R826, Punyelroo; R855, Tailem Bend; R856, Waterfall Gully; R857a–b, Fowlers Bay; R858, Paratoo; R860, Stonyfell; R861, Strathalbyn; R867a–b, Ooldea.

The three Victorian localities correspond to MV R7109, Beulah; R7125, Mallee; R7165, Mallee district, and R7131–36, Ouyen.

Additional unlocalised or poorly-localised specimens known to have been seen by Waite or available in collections at the time are AM R4978–80, MV R7176, R7185, R7192, R7197, R7202–03 (all ex WAM), WA; AM R6556 (exchanged to PNM in 1950), MV R7094, R7116, QM J2952, SAM R863, WAM R359, R629, no locality; AM R6557–58, R131180 (formerly 6393), R131181 (formerly 6416), R131182 (formerly 6422), SAM R724, R824, SA; R811, Murray Scrub, SA.

AM R6557–58 are very large adults with angulate snouts, labelled by Waite "*T. bicolor*, snout sharp-edged; put aside for comparison" (see also Waite, 1897a). Similarly angulate snouts are characteristic of large eastern Australian specimens, and appear to be an ontogenetic development, as they are absent in small individuals, while larger individuals have progressively more angulate snouts. In contrast, the nominotypic population of *R. australis* usually has a rounded snout at all growth stages (Storr, 1981).

Typhlops batillus: This species was described by Waite (1894) from a unique specimen with locality Wagga Wagga in the Macleay Museum collection. The holotype, later registered as MM R669, was transferred to the Australian Museum on permanent loan, where it is registered as R42756 (Cogger, 1979). The species was listed as distinct by Waite (1918b), Kinghorn (1929b, 1956) and Worrell (1963), none of whom reported additional material. McDowell (1974), when revising the New Guinean and Solomon Islands typhlopid fauna, examined the holotype because of a general similarity in head shape with Solomons species *R. subocularis* (Waite, 1897b), subsequently referred to the genus *Acutotyphlops* (Wallach, 1995). McDowell reported that the head was not as distinctly pointed as in Waite's (1918b) illustration, and that the holotype was female and possessed a rectal caecum. Cogger (1975 and subsequent editions) did not list the species among the Australian herpetofauna, misinterpreting McDowell's comments as suggesting that the species was not Australian (H.G. Cogger, pers. comm.). Cogger *et al.* (1983) regarded the type locality as suspect. Cogger's exclusion of the species from the Australian herpetofauna was followed by most subsequent authors (Wilson & Knowles, 1988; Swan, 1990; Weigel, 1990; Ehmann, 1992), although it was regarded as a distinct species from New South Wales by Welch (1994).

Because the holotype is female, it is not possible to definitely assign it to *Ramphotyphlops*, the genus to which all other Australian typhlopids belong, and because of the possibility that the type locality is erroneous, it is necessary to extend comparisons with other species internationally. The Macleay Museum collection contains non-Australian reptile material, including typhlopids.

I have examined the holotype of *T. batillus* and compared it to descriptions of all other typhlopid species (as listed by Hahn, 1980; Welch, 1994, with additions by Auffenberg, 1980; Rodrigues, 1991, Wallach, 1993a, 1994). In addition to the features described by Waite (1894, 1918b) and McDowell (1974), it has 557 dorsal scales, the second supralabial overlapped by the preocular, 21 subcaudal scales, and only a single elongate postocular scale. The longitudinal scales rows are 26 anteriorly (at level of 44th dorsal), reduced to 24 by the 200th dorsal, and to 22 just anterior to the vent. The eye is prominent and has an obvious pupil. Scale organs are abundantly present on the rostral, nasal, ocular, and preocular, and fewer on the frontal, supraocular, parietal, interparietal, postocular, supralabials, infralabials and some chin shields, while obvious glands are lacking along the margins of the head shields.

The species does not agree with the diagnoses of the genera *Acutotyphlops, Cyclotyphlops, Rhinotyphlops* or *Xenotyphlops* (in den Bosch & Ineich, 1994; Wallach, 1994,1995; Wallach & Ineich, 1996).

Among the species of *Ramphotyphlops*, with which it shares a T-III supralabial imbrication pattern (Wallach, 1993a,b), with the second supralabial overlapped by the preocular, it shares 24 midbody scales only with *R. acuticaudus, R. cumingii* and *R. lineatus* in Asia and the Pacific, and *R. ligatus, R. unguirostris* and *R. yirrikalae* in Australia. The three non-Australian species have fewer dorsal scales (maximum 497 for *R. cumingii*; Wallach, 1994), while all three Australian species have the nasal cleft contacting the first infralabial (*vs* second). Additionally, *R. ligatus* has fewer transverse scale rows (ventral scales up to 435; Storr, 1981) and a nasal cleft that extends parallel to the rostral well onto the dorsal surface of the head (*vs* passing medially from nostril to contact rostral, barely visible from above), *R. unguirostris* has fewer transverse scale rows (ventral scales up to 474; Storr, 1981) and an angulate snout profile, and *R. yirrikalae* has fewer dorsal scales (447–450 in the holotype and AM R12889) and a broader rostral.

Comparison with the numerous *Typhlops* species is made on a geographic basis. None of the African or European species possess the combination of a T-III supralabial imbrication, 24 midbody scales and 557 dorsal scales (Roux-Estève, 1974; Grillitsch & Grillitsch, 1993).

None of the South American species have 24 midbody scales (Peters & Orejas-Miranda, 1970; Dixon & Hendricks, 1979; Rodrigues, 1991). Although two species of Caribbean typhlopids have 24 midbody scales as a mode or occasional variant (Thomas, 1989), they also either have a posterior reduction to 22 rows of body scales well forwards of the vent and a short tail (*T. biminiensis*, Thomas, 1968), or a preocular with a strong anterior projection into the nasal, the third supralabial contacting the nasal and fewer dorsal scales (*T. dominicanus* Richmond, 1966).

Among the Malagasy and Comoran typhlopids, only *T. mucronatus* has both 24 midbody scales and a distinct eye (Guibé, 1958; Roux-Estève, 1980), and this species differs from *R. batillus* in having the nasal cleft contacting the first supralabial, and the tail as wide as long (Boettger, 1881).

Among the Asian species, only *T. bothriorhynchus, T. depressiceps, T. diardi, T. hypogius, T. klemmeri, T. kraali, T. oatesi, T. trangensis* and *T. wilsoni* have 24 midbody scales (Wall, 1908; Taylor, 1962; McDowell, 1974; Savage, 1950; Wynn & Leviton, 1993; Wallach, 1993a, 1994). All of these except the poorly-known *T. wilsoni* differ from *R.*

batillus in one or more of the following characters: dorsal scales fewer than 400, a T-V supralabial imbrication pattern, and snout profile rounded (McDowell, 1974; Wallach, 1994). As originally described, *T. wilsoni* differs from *R. batillus* in having a distinct subocular scale between ocular and supralabial (Wall, 1908).

Hence, *T. batillus* is distinct from all other described typhlopid species. Although it can not unequivocally be placed in *Ramphotyphlops*, it is most similar to that genus in the supralabial imbrication pattern. The only reported locality, Wagga Wagga, is not inconsistent with the Macleay collection history. William John Macleay was a grazier in the Riverina, owning "Kerarbury" Station, and a vineyard at Wagga Wagga. Further, he was known to have made at least one collecting trip to Wagga Wagga with his collector and curator, George Masters, in January 1874 (Fletcher, 1893; Stanbury & Holland, 1988; Horning, 1994). In the absence of any evidence to the contrary, *R. batillus* should be reinstated as a member of the Australian herpetofauna, known only from a single locality. The lack of any recent records from this district, despite herpetological collections over a number of years (Annable, 1995) is disturbing, and the conservation status of this species should be urgently evaluated.

Typhlops bituberculatus: Waite's (1918b) map differs from modern distribution maps for the species (White, 1981; Storr, 1981; Swan, 1990; Ingram & Raven, 1991) in the inclusion of records from Bundaberg, Qld, Barrow Creek, NT, eastern NSW (a dot placed about Katoomba), Fortescue River, WA, central WA (a dot placed about Lawler), and south-western WA (five dots).

The Bundaberg record is probably based on MM R444 (Bundaberg, no other data), which is confirmed as *R. bituberculatus*. The specimen is a juvenile in very poor condition. As this species in not otherwise known from eastern Queensland, with the nearest records in south-central Qld (Ingram & Raven, 1991), the record is regarded as suspect.

The Barrow Creek record is presumably based on SAM R830 (Barrows Creek, no collector, old collection), the identity of which is confirmed as *R. bituberculatus*. This specimen has about 490 dorsal scales (M. Hutchinson, pers. comm.). There are no other confirmed records of this species from the same latitude or further north, and the record should be treated as suspect.

Four of the five dots in south-western WA correspond closely to early typhlopid records subsequently reidentified (Storr, 1981) as *R. waitii*, a superficially similar species sharing a trilobed snout, 20 midbody scales and a nasal cleft proceeding from the second supralabial and which Waite was unable to identify from Boulenger's (1895) description: MV R7199, Bullsbrook (ex WAM); MV R7172, R7193, Cranbrook (ex WAM); WAM R403, Carnamah; WAM R421, Williams. The remaining locality, from the coast, may be based on AM R2429, Perth (presented by W.D. Campbell), here confirmed as *R. bituberculatus* (501 dorsal scales, 485 ventral scales, rostral not with a hooked margin), MV R7183–84, R7196, Perth, and R7190, Mortlock, Perth. Of the latter four specimens, all ex WAM and identified by Waite as *T. bituberculatus* (J. Coventry, pers. comm.), R7196 is now identified as *R. waitii*, while the remaining three specimens are confirmed as *R. bituberculatus* (G. Storr, *in litt.* to J. Coventry, pers. comm.). The locality for R2429 presumably represents a shipping point or is in error, as other reptile collections presented by Campbell either have the locality Perth but include inland species, or have the locality Boulder. The central WA record is probably based on AM R3355 (now AMNH 20942), Lawler (pre: G. Shipton). The Fortescue River record is probably based on SAM R220 (Fortescue River, W.D. Dodd), although that specimen is apparently lost. The record is within the range of *R. waitii* (Storr, 1981), and is presumed to be based on that species. The remaining WA locality, within the known modern range of the species (Storr, 1981), is probably based on AM R153051 (formerly part of R1693), Coolgardie, together with two poorly localised specimens, WAM R26, R448 ("Goldfields").

The basis for the eastern NSW locality remains difficult to determine. There are two records of *R. bituberculatus* from eastern NSW, although neither fit the mapped locality precisely. AM R64, Callan Park (a Sydney locality), was originally identified as *Pygopus lepidopodus*, but subsequently reidentified as *R. bituberculatus* in Waite's handwriting. This record is rejected, due to the lack of confirmatory records from east of the Great Dividing Range and the potential for association of the wrong specimen with the tag suggested by the change in identification. The second record is AM R131179 (formerly A2475), from Mr Walter Blaxland's Station, the identification being initialled by Waite. The collection of which this specimen is part is annotated in the original register with what appears to read "Cullingral, Merriwa".

Identifiable specimens corresponding to most of Waite's other NSW dots are: AM R1693, Dubbo; R2723, Broken Hill; R1176, Menindee; R3551, Narrandera; R3640, Lake Cargelligo; R4259 (now AMNH 20948), Shuttleton; R4403, N Broken Hill; R5109–10, Corella, nr Brewarrina; MM R670, Wilcannia; R671, Coonabarabran; SAM R831a–h, Silverton; MV R7071, Jerilderie and MV R7086, Deniliquin. One specimen with a precise locality, AM R1448, Tocumwal, does not appear on his 1918 map.

The ten Victorian localities, all within the modern range, correspond in part to the following specimens: MV R7060, "Bathry" Stn, Terricks; R7065, R7126–33, R7137, Ouyen; R7076, Beulah; R7078, Mallee; R7085, Gunbower; R7092, Myall, via Koondrook; R7100, near Gerang; R7106, Nhill; R7138–43, Woomelang, although one specimen seen by Waite, MV R7083, Goulburn Valley, is not mapped, I have been unable to identify the locality for another (R7064, Cashel), and the southernmost locality cannot be related to a specimen.

South Australian records corresponding to Waite's map localities are: SAM R541, R832–34 (R834 now missing), Murray Bridge; R547, Yorke Peninsula; R617, Kadina; R630 (now missing), Streaky Bay; R646 (now missing), Quorn; R656, Modbury; R667, 408 Mile, East-West Line; R813, Pt Lincoln; R828, Kopperamanna, Coopers Ck; R829 (now missing), Semaphore; R834a–b, Purnong; R835, Ardrossan; R836 (now missing), Denial Bay; R837, Roseworthy; R839a–b, Leigh Creek; R840, Oodlawirra; R841, Kadina; R842, Yudnamutana; R843a–b (now missing), Orroroo; R844, Kapunda; R845, Pt Pirie; R846a–

e, between Ooldea and Talarinna (only a–c now present); R847, Kilalpaninna; R887 (now missing), Reedbeds. One SA specimen available to Waite, but not mapped is SAM R540, Pernatty Lagoon. Waite localities for which specimens are not identifiable include several peripheral localities in a cluster about Adelaide and the Murray region to the east, and the two north-easternmost localities in the state, one of which probably corresponds to Strzelecki Ck (Waite, 1917).

Additional to these are the following poorly-localised specimens of the same vintage: AM 6418 (not found), R1917, R6559, R131171–73 (formerly 5180), R131174 (formerly 6406), R131175–78 (formerly 6417, 6419–20, 6423), MV 7099, SAM R848 (36 specimens, destroyed 1965), no locality; AM R1451 (7 specimens), Darling River floods; R5027, MM R672–73, QM J1914 (formerly AM R1567), NSW; AM R6585, interior of NSW?; R131175–78 (previously 6417, 6419–20, 6423), SAM R217, R301, SA; MV R7103, Vic; R7204, WA; SAM R838a–e, Murray Scrub, SA.

One specimen potentially available to Waite does not correspond to a map locality: QM J1915, Roma, Qld. The registration entry for this specimen is annotated "on exhibit, removed 1954", and it was presumably not sent to Waite.

Typhlops broomi: Waite (1918b) reported examining five specimens, and gave the localities Cairns, Norseman, Broome and Mallee, Vic., the latter three well outside the known modern range (Ingram & Covacevich, 1993; Shea, 1995). The Cairns locality is probably based on SAM R851, Cairns (A.M. Lea, old collection, registered 11.i.1918). The Broome record is based on a specimen of *R. diversus*, SAM R925 (previously MV R7182, itself received from WAM) from Rowe, Broome, initially identified as *R. broomi*. The Norseman record is based on MV R7066, identified by Waite as *R. broomi*, but reidentified as *R. australis* (Storr, 1981). The fourth locality, "Mallee, Vic." is based on MV R7170 (Mallee district, C. Frost per J. Frost), data which appears on a number of MV specimens of dubious provenance, including other typhlopids. The record was rejected by Robertson *et al.* (1989) and Coventry & Robertson (1991). The remaining specimen available to Waite (AM R2034, north Queensland) was identified by Shea (1995). Two additional specimens, QM J2953–54 (Stannary Hills, nr Herberton) were potentially available on the basis of registration date, but were either not seen or overlooked by Waite.

Typhlops diversus: Waite (1918b) stated that he had examined four specimens, but indicated five localities on his map. Two of these correspond to previous literature records: the type of *Typhlops ammodytes* from the Monte Bello Islands, and two specimens from Noonkambah in the Kimberley reported by Lönnberg & Andersson (1913), the latter based on NHRM 2396–97, which I confirm as *R. diversus*. The type locality, Morven, Qld (given as Mowen by Waite, 1894, but subsequently corrected by Waite, 1918), corresponds to the only Queensland locality mapped, while the remaining two map localities are in the Northern Territory, one in the Darwin area and the other about Tennant Creek. The latter two records are probably based on SAM R862, (Tennant Creek, J.F. Field) and one of QM J2590–91 (Darwin, G.F. Hill). J2590–91 are misidentified *R. tovelli* (K. Aplin, pers. comm.). The fourth specimen, not corresponding to a map locality, is MV R7112 (no data).

Typhlops endoterus: Waite (1918b) described this new species from three specimens from Hermannsburg, but gave the number of only the holotype (SAM R88). The two paratypes (SAM R87, R89) were identified by Houston (1976).

Typhlops grypus: Waite (1918b), when describing the species, stated that he had four specimens, the type in the Museum of Victoria, the others in the Queensland Museum and South Australian Museum. Of the four, one was from Marble Bar, one was from "Gregory Downs", and two lacked localities. The holotype (MV R7102, now D12351) lacks locality data. A second MV specimen, R7200 (now D12358), from Marble Bar, was identified as a paratype by Coventry (1970), who noted that correspondence from Waite proved that the specimen was available to him at the time of description. Hence, one of the other two specimens, which are paratypes, must be from "Gregory Downs", the other lacking locality data, and they must be in the Queensland and South Australian Museums. The only specimen in the latter collection available at the time of Waite's revision is SAM R849, no locality apart from the enigmatic comment "in stomach of spec at Semaphore", and presented by Dr Wylde. There are four early QM typhlopids with locality "Gregory Downs": J2944–47. Of these J2945 was destroyed in 1953 without any identification. The remaining three are all *R. grypus*. Only J2947 is annotated as identified by Waite and must be the remaining paratype. Presumably Waite was only sent one of the series.

Typhlops guentheri: Waite's map (1918b) has four localities. Three of these correspond to literature records (Daly River; Boulenger, 1895) or early specimen records (AM A4872 [now R150870], QM J2266, Pt Darwin; MV R7073, Oenpelli, East Alligator River) corresponding to the known distribution (Shea & Horner, 1997). The remaining locality is identified as Marble Bar in Waite's description. The record corresponds to WAM R535 (Marble Bar), first registration identification *T. nigricauda*, identified by Waite as *T. guentheri*. This specimen was subsequently reidentified as *R. affinis* by G. Storr (annotation in register), but was not listed by Storr (1981). It was later reidentified as probably *R. grypus* by L. Smith in 1990 but cannot now be found to verify the identification (L. Smith, pers. comm.). The first identification of this species as *T. nigricauda* suggests that the tail was black, and the later identification as *R. affinis* suggests that the snout was at least angulate. These two features suggest that the record is a misidentified *R. grypus*. Four additional specimens (AM R2292 (ex SAM), MV R7111, SAM R802a–b, all no data) are known to have been identified by Waite as *R. guentheri*. Of Waite's *guentheri* records, AM R2292, R150870 and SAM R802b have been subsequently reidentified (Shea & Horner, 1997) as *R. nema*.

Typhlops kenti: Waite (1918b) examined four specimens of this species, since synonymised with *R. affinis* (McDowell, 1974): from King's Sound, Broome, "Yanyereddy" Station (near Ashburton River) and "Western Australia". All are well beyond the known distribution of *R. affinis*. Waite stated that "in three specimens the tail is black, in one other the head is also black". These black markings indicate that Waite's specimens were *R. grypus*, (Parker, 1931, as *T. nigroterminatus*). Two of his records are based on MV R7187 (ex WAM), Rowe, Broome and MM R683, King Sound, both specimens of *R. grypus*. Possibly the "Yanyereddy" Station record is based on SAM R804, a specimen of *R. grypus* (original identification *T. kenti*) from between the Ashburton and Gascoign [sic] Rivers, 1895, P. St. Barbe-Ayliffe. The remaining poorly localised specimen corresponds to MV R7179 (WA). One additional specimen, WAM R145 (Derby) was present in the WAM collection at the time, but is not identified as examined by Waite, and does not correspond to his listed localities.

Typhlops labialis: This species was described by Waite (1918b) from a unique specimen (WAM R630) with locality stated as Western Australia. Although it appears as a valid species in several subsequent publications (Kinghorn, 1929b, 1956; Glauert, 1950; Worrell, 1963), the name was synonymised with the widespread Asian species *Typhlops diardi* by McDowell (1974). The Western Australian locality is erroneous, as the holotype lacks any associated data (McDowell, 1974).

Typhlops ligatus: One specimen mapped from north-west Victoria is well beyond the known range in northern NSW, Qld, NT and the Kimberley (Wells, 1979; Storr, 1981; Swan, 1990; Ingram & Raven, 1991). The source for this record is presumably SAM R921 (ex MV R7167) and MV R7168 (Mallee, Victoria), the latter noted by Rawlinson (1966). A locality in western NSW mapped by Waite, west of localities mapped by Swan (1990) in NSW, is probably based on MM R446 (2 specimens), "Wonaminta", nr Wilcannia, here confirmed as *R. ligatus*. The specimens are juveniles in poor condition, but dorsal scale counts are approximately 317–323 for the two. The Victorian records are from an imprecise locality associated with several other species not subsequently confirmed from the area (*R. broomi, R. nigrescens, R. pinguis, R. proximus, R. unguirostris*), and are treated as erroneous. The western New South Wales record, however, although similarly not confirmed by recent material, is from a poorly collected area, and should continue to be treated as valid until evidence to the contrary becomes available.

Six of the remaining seven localities mapped by Waite (1918b), in northern NSW and eastern Qld, correspond to AM R153040 (formerly A10637), Coomooboolaroo, Qld (Waite, 1893); R3970, Brewarrina, NSW; QM J1212, Wycombe, Surat, Qld; J2828, "Lochnagar", Central Railway Line, via Barcaldine, Qld; J2940, Rockhampton, Qld; SAM R197, Buff, Rockhampton, Qld; R850, Niall, "Delta" Stn, Alice, Qld, and the type locality (Mackay), all within the currently known distribution of the species. One other mapped locality, north-west of Brewarrina, cannot be associated with specimens, unless it is a misplaced Lightning Ridge (AM R6716). To the above-listed specimens can be added the holotype of *Typhlops curtus* (AM R1132), examined by Waite (1893). The type locality (Walsh River) was presumably considered too imprecise to map (Waite, 1918b: 14). Also known to have been seen is MV R7068 (Qld). Three other specimens with imprecise localities were available in collections examined by Waite: AM R153038–39 (formerly 5179, 6405; no locality); QM J2048 (destroyed 1964; probably Qld); J2742 (central Qld); J2941 (destroyed 1965, no locality), although it cannot be confirmed that they were seen by Waite.

Four specimens of appropriate vintage with localities in south-eastern Qld (QM J623, Brisbane, Qld; J624, Dalby, Qld; J2939, Toowong, Brisbane, Qld; SAM R50, Lowood, Qld) do not correspond to localities on Waite's map. The number of localities and variety of sources of these specimens suggest that Waite's map was incomplete in this instance, rather than that he did not see this material.

Typhlops pinguis: Waite (1897a) described this species from a single specimen from an unidentified locality in South Australia, the holotype being identified by Waite (1918b) as SAM R803 (registered in 1918; Houston, 1976). Waite (1918b) identified a second specimen from Mallee, Victoria, and mapped four localities in far south-western Australia. The species is now known only from the latter region (Storr, 1981). The Mallee specimen is SAM R922 (previously MV R7166, Mallee, Victoria), while six other early specimens fit three of the four map localities in Western Australia: MV R7173 (ex WAM), Wokalup; SAM R924 (ex WAM R426), Capel; SAM R923 (ex MV R7174, itself ex WAM), WAM R473, Katanning; WAM R590, Kojonup and WAM R624, Wickepin (assuming Wokalup and Capel are represented by a single dot). All but the last specimen were examined and their identity confirmed by Storr (1981). Four other poorly localised specimens were seen by Waite: MV R7175, R7180, R7195, R7201 (all from WA, ex WAM), and two other specimens with the same locality (AM R4976–77, not found) may have been seen by him.

Typhlops polygrammicus: Waite's (1918b) concept of *T. polygrammicus* is now known as *R. nigrescens*, following Smith (1927). Waite's distribution map for this species closely approximates the distribution based on modern records (Swan, 1990; Coventry & Robertson, 1991; Ingram & Raven, 1991) except for the two westernmost localities in Victoria and a record from extreme south-east New South Wales. The latter is probably based on SAM R917 (ex AM R1790), Twofold Bay and AM R2295–96 (not found), Bega (R. Etheridge).

Specimens corresponding to localities in the main body of the species' distribution in NSW include AM R905, West Bargo; R1093, R1602, R2027 (not found), R5183, Walcha (R1093 sent to R.M. Bousek in 1925; R1602 now CAS 77814–15); R1521 (not found), Warri, via Braidwood; R1574, R1734 (destroyed 1965), Kempsey; R2412–14, Murwillumbah; R2720, Armidale (now CAS 77816); R4189, Mudgee district; R5975–76, Broughton I.; R6567–70, Tharwa (collected by Waite; R6567 now AMNH 20946;

R6568 not found); R131153, Port Macquarie (formerly 6394); R131170, Mittagong (formerly B9905), and a number of specimens from Sydney suburbs, which are represented by a single dot (Waite, 1918b: 14). It is not possible to unequivocally determine which of the many AM specimens from Sydney listed in the early registers were examined by Waite. However, at least the following Sydney specimens are annotated "examined by Waite 1918": R5, Woolahra; R8, Hunters Hill; R108, Homebush; R398, Randwick; R780, Auburn; R1405, Waverley; R1442, Marrickville; R6554–55, Penrith, while the following additional Sydney region specimens were registered pre-1918 and, in the absence of contrary data, presumably available post-1914 to have been sent to Waite: A8920 (now CAS 77812), R131149 (formerly 5175), R131154–55 (formerly 6398–99), R1311161–62 (formerly A238, A522), Sydney; R625, South Creek, St Mary's; R673 (not found), Riverstone; R674 (not found), Bulli; R1189 (not found), Granville; R1246 (not found), Campbelltown; R1610 (not found), Cabramatta; R1664, N Sydney; R1927, Waverley; R2173 (not found), nr Liverpool; R2301 (destroyed 1965), R3787 (destroyed 1924), Penrith; R2376, Balmain; R2518, Mosman; R2532 (now AMNH 20943), South Head; R3208–10 (only R3209 found), Fairfield; R3655 (now AMNH 20944), Coogee; R3659 (now CAS 77813), Alexandria; R4573, Randwick; R4599, Mosman Bay; R4622, Freshwater; R4816, Bellevue Hill; R5393, Camden; R5971, Lakemba; R131164 (formerly A2813), Smithfield; R131165 (formerly A6386), Woolahra; R131167 (formerly A8924), Kogarah; R131169 (formerly B3704), Field of Mars. Added to these is MM R677, Sydney ("examined ERW").

Nine additional early specimens from NSW which do not correspond to a map dot (AM R911, R1452, MM R678, Richmond River; MV R7096, Clarence River; R7119–23, Macleay River) were presumably excluded because of the imprecise localities (the first is identified in the registers as the basis for the figure of the tail of *T. ruppelli* in Waite, 1893). Conversely, two specimens (R1460, Bendenine; R2719, Salisbury Plains) are annotated as examined by Waite, but do not correspond to map localities, and there are three mapped localities in NSW within the modern range for which corresponding specimens cannot be identified.

Victorian specimens corresponding to Waite's map dots are: MV R3081, Kewell; R7057, Tallangatta; R7059, Mallee; R7074, Alexandra; R7079, R7113, Bright; R7087, Goulburn, and R7090, Tooboorac, although no specimen can be found to correspond with one of the western Victorian localities.

The single Queensland dot, about Brisbane, corresponds to QM J2874, J2884, Tamborine Mtn; J2875, St Helena I., and J2942, Brisbane, of which the first is definitely recorded as examined by Waite.

Other poorly localised specimen known to have been seen by Waite, or available pre-1917 and probably post-1914 are: AM R7 (not found), R90, R126 (not found), R955, R1068 (now SAM R919), R1092(not found), R1121, R2547–48, R2550–53, R2572, R2577 (not found), R2721, R2728, R3859 (now SAM R918), R6021, R6023–25, R6566, R6571–80 (R6572, R6580 not found), R131150–51 (formerly 5176–77), R131156–58 (formerly 6400, 6402, 6404), MV R7061, R7110, no locality; AM R1229 (not found), R1235, NSW?; R131159–60 (formerly 6407–08), R131163 (formerly A1872), MM R674–76, MV R7081, NSW; R7091, Vic; QM J1931–33 (destroyed or not found 1965), Qld; J1935–36 (destroyed or not found 1965), Qld or NSW; J2049 (destroyed 1964), probably Qld.

One specimen present in early collections, but not mapped or mentioned by Waite, presumably rejected without comment because of its distance from other records if indeed it was seen, is AM R131168 (formerly A10182), Nicol [=Nickol] Bay, WA.

Typhlops proximus: This species was described by Waite (1893), who nominated AM 6411 (now R131704), from NSW, as holotype, but noted that he had several specimens available to him. Specimens of *R. proximus* in the Australian Museum registered prior to 1893, and hence available to Waite and potentially paratypes are: 5181 (not found), R95 (now SAM R915, skeletonised), R1115, (exchanged with R.M. Bousek in 1923); R145401 (formerly 5171), R145404 (formerly 6403), R145407 (formerly B2309), no locality; 6415 (exchanged to Baylor University 1905), R145403 (formerly AM 6397), R145405–06 (formerly 6412, 6415), NSW; R615, Richmond; R1028 (not found), Wallinbillan [=Wallanbillan], and R145402 (formerly 6396), West Maitland.

Waite (1918b) maps a relatively continuous distribution in south-eastern Australia, corresponding to the known modern distribution (Swan, 1990; Coventry & Robertson, 1991; Ingram & Raven, 1991), but with three outlying localities, one in north Queensland, one in western NSW and one in north-western Victoria. The north Queensland locality on the map corresponds to the text reference to a distribution south of 17°05'S, and is probably based on the specimen from Malanda (17°22'S) reported by Lönnberg & Andersson (1915). This record is based on NHRM 22456, the identity of which is confirmed as *R. proximus*. Two other specimens are known from the same region (McDowell, 1974: AMNH 27263, Ravenshoe district; AM R148795, 8.2km ESE Ravenshoe, Herberton district), validating this record, although a literature record from further north (Ingram & Raven, 1991, based on J38221, "Silver Plains") is based on a misidentified *R. unguirostris* (P. Couper, pers. comm.). The Atherton Tableland population appears to be isolated from the main distribution, and may have greater dorsal scale counts (390 for R148795, 392 for NHRM 22456 *vs* 326–378, $\bar{x}$ = 349.9, SD = 13.16, n = 62; latter based on AM R1497, R1570, R1845, R2343, R2722, R2724, R2727, R3440, R5764, R6560, R6562, R6564, R7221, R7982, R8440, R8982, R10182, R10437, R10776, R10786, R11498, R11693, R12255, R12307, R12526, R13115, R13448, R13661, R13779, R13830, R13835, R14821, R14946, R15218, R15868, R15936, R17915–16, R18289, R18886, R27304–05, R27313, R30331, R49083, R64294, R66665, R86811, R92391–93, R95270, R95458, R111876, R114565, R118650, R122967, R123430, R128510, R132486, R144603, R144776).

The basis for Waite's western NSW locality, a dot in the vicinity of Tilpa, is not known, as it does not correspond to any identifiable specimen in early collections, unless the

dot represents the Darling River generally (AM R6561, now AMNH 20947, Darling River). The north-western Victorian record is probably based on SAM R922 (Mallee area, Vic), and is probably erroneous, as with other records from this locality.

Other specimens that were available to Waite, and correspond to localities on his map, are, in addition to the localities cited above: AM R1497, R1845, SAM R914 (ex AM R1844), Moree, NSW; AM R1570, R2343, Murrumburrah, NSW; R3440, Manilla, NSW; R5764, Tamworth, NSW; MV R3080, Charlton, Vic; R7067, Macorna, Vic; R7070, Murchison, Vic; R7076, Beulah, Vic; R7082, R7108, R7115, Wangaratta, Vic; R7105, 50mi W Toowoomba, Qld; QM J237 (destroyed), Wondai, Qld; J239, Clayfield, Brisbane, Qld; J362, Woodford, Qld; J1904, Bundaberg, Qld; J2935, Dalby, Qld; J2936, Goodna, Brisbane, Qld; J2937, Glasshouse Mtns, Qld; SAM R200, Mungar Junction, Qld; SAM R916 (ex AM R5690), Budden, Rylstone, NSW. Also seen by Waite (register annotations) are AM R2724, R6560, R6562, R6564, QM J3004, no locality. Three map localities, in the vicinity of Glen Innes, NSW, the north-easternmost NSW locality and the easternmost Victorian locality, cannot be associated with specimens.

Localities for two of the potential paratypes (Richmond and Wallanbillan), together with three MV specimens known to have been examined by Waite (R7077, Moora South, Vic; R7094, Kewell, Vic; R7101, "Nauranny", Murrumbidgee, NSW) do not appear on Waite's map. Wallanbillan, Moora South and "Nauranny" may not have been identifiable by Waite, while he may have confused Richmond with Richmond River, possibly corresponding with the otherwise unreconcilable dot in north-eastern NSW on his map.

Other poorly-localised specimens that may have been seen by Waite are: AM R2727; QM J2938 (destroyed 1965), no locality, and J1934 (destroyed 1965), Qld.

Typhlops torresianus: Waite's concept of *torresianus* equates to the species *R. polygrammicus* of most subsequent authors. Queensland Museum records (Ingram & Raven, 1991) and Australian Museum material of this species are solely from north-eastern Queensland, as are the majority of Waite's records. Waite maps one locality in south-eastern Qld. The basis for this record is QM J3006 (Brisbane), original identification *T. torresianus*, current identification *R. polygrammicus*. This species is very similar to *R. nigrescens* (Waite's *T. polygrammicus*), differing primarily in the origin of the nasal cleft (from the first supralabial in *nigrescens*, from the second in *polygrammicus*), and it is possible that the specimen is an aberrant *R. nigrescens*.

Other specimens of *R. polygrammicus* potentially available to Waite or known to have been examined by him, and corresponding to his map localities are: AM R1083, Bellenden Ker Range; R1926 (not found), Ripple Creek, Herbert River; R4691, Dunk I.; MM R685, Cape Grenville (now in very poor condition); MV R7117, Kuranda; QM J2273, Gordonvale and SAM R927 (ex MV R7095), Qld, assuming that R1083, R1926, R7117 and J2273 are represented by a single dot. The remaining mapped locality is presumably Murray Island, type locality of *T. torresianus*.

Storr (1981: 256) is the only modern author to maintain usage of *R. torresianus* as distinct from *R. polygrammicus* from Timor, and justified his usage by claiming *R. torresianus* has fewer longitudinal scale rows (ventrals "c.350" *vs* 421–450). Among 12 specimens from north-eastern Australia (AM R1083, R4691, R9614, R10828, R15137, R57282, R57826, R65225, R82599, R98337, R107055, R127404), I find 370–422 dorsal scales, with higher counts predominating in the Cairns region, and lower counts in the drier country on western Cape York. These data suggest that the difference between the two forms is less than previously stated, and geographically variable. Hence, in the absence of a more rigorous study of variation throughout the range, I prefer to treat the two as conspecific.

Typhlops unguirostris: Waite had very few records for this species, providing four localities on his map, and noting that he had examined specimens from the type locality (Rockhampton), Darwin, Lyndoch Valley, SA and Mallee, Victoria. The Darwin locality corresponds to the map, and is probably based on AM R4582, Port Darwin. There are two mapped localities in Queensland, one corresponding to Rockhampton (MV R7058), the other to Port Bowen (= Port Clinton), type locality for the synonym *Typhlops curvirostris*. These three localities are within the modern known range of the species in tropical Australia (Storr, 1981; Ingram & Raven, 1991). However, the other two localities are well beyond this distribution. The Lyndoch Valley locality does not appear on Waite's map. The record is undoubtedly based on AM R6581–82 (Lyndoch Valley, SA, Dr Richters, "old collection"). The Mallee, Victoria locality is presumably based on MV R7080 (Rawlinson, 1966). The specimens for both records are identifiable as typical *R. unguirostris* (24 midbody scales, nasal cleft from first supralabial, angulate and strongly-projecting snout, dorsal scales 502, 477, 515 respectively), but are probably incorrectly localised.

One additional specimen, present in the Australian Museum collection from 1894, does not appear to have been used by Waite: AM R1568, Cambridge Gulf (ex QM), unless it was the basis for one of the otherwise unidentifiable *R. wiedii* records from the Kimberley. This specimen is presumably that cited by de Vis (1889). Another specimen, QM J3005, lacking locality data and destroyed in 1965, may also have been available to Waite.

Typhlops wiedii: The map provided by Waite (1918b) indicates a much more extensive distribution than that demonstrated by recent studies (Ingram & Raven, 1991; Shea, 1995). Beyond recent limits are two localities in the Kimberley (one about Wyndham, the other about "Theda"), one in Torres Strait, one near the tip of Cape York, one in the vicinity of Cooktown, one about Bowen, four in the south-west of WA about Perth, and one in the Western Australian goldfields.

The Cape York and Torres Strait records are probably based on *R. leucoproctus* (Boulenger, 1893). Waite (1894) had evidently regarded this as a distinct species, but he later listed it as a synonym of *R. wiedii* (Waite, 1918b). The

species was subsequently resurrected by McDowell (1974). Although the two species are superficially similar, they are allopatrically distributed, and are readily differentiated on colour (dark both dorsally and ventrally in *leucoproctus*, pale both dorsally and ventrally in *wiedii*), and have significantly different numbers of dorsal scales (*leucoproctus* 377–394, $\bar{x}$ = 383.8, SD = 6.30, n = 8, based on AM R4537, R7956, R42661, R48541, R55678, R58961, R59060, R97853; *wiedii* 381–439, $\bar{x}$ = 417.8, SD = 17.88, n = 10, based on AM R1846, R2001, R2729, R4122, R4544, R5908, R6344, R6563, R6565, R6584; Mann-Whitney U test, U = 75, p = 0.002). Two specimens of *R. leucoproctus* available to Waite, AM R4537, Somerset and MM R679, Darnley I, fit Waite's dots. Another specimen, MM R684, Darnley I., may have been seen by Waite, although there is no record of this with the specimen.

The Cooktown locality is presumably based on MCZ 6487 (Cooktown), identified by Garman (1901) as *R. wiedii*. This specimen was subsequently reidentified (Loveridge, 1934) as *R. affinis*, and by McDowell (1974) as *R. broomi*.

The other odd eastern Australian record, about Bowen, is presumably based on MM R442, Pt Denison (no collector recorded, but probably either George Masters, who collected at this locality for both the Macleay Museum and Australian Museum in 1861/62, or Edward Dämel, who collected at this locality in 1865–66; Fletcher, 1893; Stanbury & Holland, 1988; Tilbrook, 1992). There appears to be no reason to doubt the accuracy of the locality data for this specimen.

The south-west Australian localities are based on misidentified *R. australis*, which share with *R. wiedii* 20 midbody scales and a nasal cleft from the second supralabial and not dividing the nostril. Specimens from south-west WA registered as identified by Waite as *T. wiedii* are: WAM R410, North Jandakot (two of seven specimens originally under this number now SAM R926a–b); R457, Muchea; R507, Mundaring. These records correspond to three of four dots in this area. R457 was not examined by Storr (1981) and is apparently lost. The remaining dot, placed about Perth, is probably based on one or more of the several *R. australis* records from Perth (see above). One additional unlocalised WA specimen of *R. australis* (MV R7198) also bears the Waite identification *T. wiedii*.

The Goldfields record, to the south of Kalgoorlie, and north of Norseman (based on Waite's maps for *australis* and *broomi*) is based on WAM R318, Widgiemooltha, likewise a specimen of *R. australis* (Storr, 1981).

One of the Kimberley records is probably based on WAM R485, Forest River Mission (J.A. Dobson), identified by Waite in the register as *T. wiedii*. This specimen was not examined by Storr (1981), and is apparently lost. However, it is worth noting that two recently described Kimberley species, *R. kimberleyensis* and *R. troglodytes*, share with *R. wiedii* 22 midbody scales and a nasal cleft contacting the second supralabial (Storr, 1981). The source for the other Kimberley record is uncertain, unless it is based on a specimen of *R. unguirostris* (AM R1568) not otherwise mapped (see above). If this is the case, the error must be considered typographical, as it is not conceivable that Waite would have confused the two very different species.

Waite's other mapped localities for *R. wiedii*, within the modern distribution, are at least partly based on the following specimens: AM R782 (now AMNH 20950), R6586, Yandenbah, NSW; R1441, R3339 (not found), Dubbo, NSW; R1846, Moree, NSW; R2001, Quirindi, NSW; R4122, Clarence River, NSW; R4544, Boggabri, NSW; R5908, R6344, QM J2197–98, Eidsvold, Qld; MV R7097, Grafton, NSW; MV R7107, Pine River, Qld; QM J171, J2087, J2949, Brisbane, Qld; J890–91, Enoggera, Brisbane, Qld; J1235 (destroyed 1964), Booval, Ipswich, Qld; J2130–32, Corinda, Brisbane, Qld; J2432–33, 17 Mile Rocks, Brisbane, Qld, and J2948, Breakfast Ck, Hamilton, Qld, assuming the latter seven localities and the type locality (Brisbane) are represented by a single dot.

Other specimens that were or may have been seen by Waite, but are not mapped, are AM R1453 (currently 12 specimens, but some destroyed 1914), Darling River floods, NSW; R1596, Qld; R2729, R6563, R6565, R6584, R6587–88, MV R7144–46, QM J2445 (destroyed 1953), no locality; AM R3600, Koorawatha, NSW (registration entry notes "identified by Waite 1918"); MM R680–81 (5 specimens), Tamworth, NSW; QM J2045–47, J2059–60 (all five destroyed 1964), probably Qld; J2115, Oakey, Qld; J2730–31 (latter specimen exchanged to PNM), Pittsworth, Pampas, Qld; J2920–2921, Bowenville district, Qld. The lack of a dot in the Darling Downs on Waite's map, despite records from the latter three localities, probably represents an error on Waite's part.

Non-Australian species. Although Waite primarily worked on the Australian typhlopid fauna, he described two non-Australian species (*Typhlops subocularis* Waite, 1897b, and *Typhlops infralabialis* Waite, 1918a, both now in *Acutotyphlops*; Wallach, 1995) and reported typhlopids from Fiji (Waite, 1898). The holotypes of both new species were re-described by Wallach (1995) who, following Cogger (1979), reported that the paratype of the former species was missing. I also have been unable to locate AM R2203, identified as the paratype by register entry. However, R2169 (no locality, E. Sutton), a specimen of the same species, accurately fits the measurements provided by Waite (1897b) for the paratype and may be the missing specimen with the wrong tag attached.

Wallach (1996) could not determine the basis for Waite's Fijian typhlopid record. Register entries for AM 6428–30 state "*Typhlops* nov. sp. Wai Obi, Vanua Pi, Fiji, Mr J. Johnston, Fiji". Additionally "(Naota)" is entered against 6430. These data correspond to those presented by Waite (1898). Unfortunately, 6428 is further annotated as destroyed 1914, and the other two specimens cannot be found, and may have shared the same fate.

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The Scincid Lizard Genus *Caledoniscincus* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: A Review of *Caledoniscincus austrocaledonicus* (Bavay) and Description of Six New Species from Province Nord

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ABSTRACT. The status of the New Caledonian scincid lizard *Caledoniscincus austrocaledonicus* (Bavay) is reviewed and found to comprise two species. The species conspecific with the designated neotype is widespread and morphologically diverse, the other is conspecific with *Euprepes haplorhinus* Günther and is also widespread in distribution. These two species occur in sympatry over much of their range, particularly on the west coast. Six new species of *Caledoniscincus* are described from the central and northern regions of the island, bringing to eleven the total number of species in the genus. The new species are restricted to closed forest habitat and have limited distributions, hence they are all regarded as vulnerable to disturbance of this habitat type. The eight species dealt with in this paper are recognised on the basis of combined morphological and genetic (allozyme) analysis of 36 populations representing all members in the genus.

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Some of the most common and widespread elements of the New Caledonian lizard fauna are the small scincid species in the genus *Caledoniscincus*. The last revision of the genus (Sadlier, 1986) identified four species, *C. austrocaledonicus, C. atropunctatus, C. festivus*, and *C. orestes*, all characterised by marked sexual dimorphism in colour and pattern. *Caledoniscincus austrocaledonicus, C. festivus* and *C. atropunctatus* are widespread throughout the island, whereas *C. orestes* at the time of description (1986) was only known from mid-high (600–1,400 m asl) habitats on

Mt Panié in the northeast ranges. The four species were distinguished from one another mainly by coloration (particularly that of males) and size.

Extensive field research in New Caledonia over the past 5 years has revealed *Caledoniscincus* to be a far more diverse group than previously suspected. The widespread species *C. austrocaledonicus* has been found to comprise two species, one of which is conspecific with *Euprepes haplorhinus* Günther (formerly a synonym of *C. austrocaledonicus*). In the central and northern regions of the island six new taxa are known from areas of closed forest habitat. Several of the undescribed species are known from only single localities or small geographical areas, while the remainder are restricted to larger, but still discrete regions. In a south to north order the new species described are: *C. cryptos* known only from a single specimen in the central ranges (near Col d'Amieu); *C. renevieri* known from several localities in the central ranges (Col des Roussettes, Mt Aoupinié, and Grottes des Adio); *C. chazeaui* from one, possibly two, locations near limestone outcrops on the northeast coast (near Hienghène); *C. aquilonius* from a number of localities in the northern ranges; *C. auratus* from one, possibly two, locations near limestone outcrops on the northwest coast (near Koumac); and *C. terma* known only from Mt Mandjélia at the northern tip of the northeast ranges. Because of the localised nature of their distributions and the range of threats to closed forest habitat in New Caledonia, most of the new taxa described in this paper are considered to be of particular conservation concern.

Materials and methods

Abbreviations. Institutional abbreviations are as follows: Australian Museum (AMS); The Natural History Museum, London (BMNH); California Academy of Sciences (CAS); Naturhistorisches Museum, Basel (NHMB); Muséum national d'Histoire naturelle, Paris (MNHN).

The full suite of morphological characters listed below were scored for each specimen where possible. For each character the abbreviation used in Table 3 is given in parentheses.

Measurements. Snout to vent length (SVL)—measured from tip of snout to caudal edge of anal scales; axilla to groin distance—measured from middle of base of forelimb to middle of base of hindlimb; forelimb to snout length—measured from tip of snout to middle of base of forelimb; hindlimb length—measured from middle of base of hindlimb to tip of fourth toe including nail; tail length (TL)—measured from caudal edge of anal scales to tip of tail, on complete original tails only. Body measurements (axilla to groin, forelimb to snout, hindlimb, and tail lengths) are for adults only, as determined by reproductive maturity (presence of enlarged yolked ovarian follicles or eggs in females, and presence of enlarged testes and distinctive coloration in males) and/or obvious size classes, and are expressed as percentages of snout to vent length in the taxon accounts.

Scalation. Midbody scale rows (MBR)—number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scales (DSR)—number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at level of vent opening; fourth finger and toe scales—number of dorsal scales on fourth digit of hand and foot, distal scale contains claw and basal scale broadly contacts adjacent basal scale of third finger or toe; fourth finger and toe lamellae—number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at, or proximal to, a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides and the mean value used in description of each species; in the holotype descriptions these values are presented as left/right values. Sexual dimorphism in paravertebral scales (the scalation character most likely to exhibit this trait) was assessed using independent two-sample *t*-test in those species represented by a moderately large sample size (=10 specimens with approximately equal numbers of each sex). Variation between populations was assessed using independent two-sample *t*-tests for all scalation characters. However, only characters with a high P value ($P \leq 0.001$) are given in the comparison of species as these most likely reflect unambiguous species level differences.

Osteology. Specimens were *X*-rayed for counting the number of presacral vertebrae and postsacral vertebrae (complete original tails only).

Electrophoretic methods. Standard methods for cellulose acetate electrophoresis of liver homogenates on TITAN III plates (Helena Laboratories) were used to assess genetic relationships between populations (Hebert & Beaton, 1989; Colgan & Flannery, 1992; Sadlier *et al.*, 1993). Where more than one locus encoding the same enzyme was found, they are designated numerically in order of decreasing anodal mobility. Allozymes are designated (alphabetically) in the same fashion for each locus. The computer package BIOSYS-1 (Swofford & Selander, 1981) was used to calculate genetic distances and to perform cluster analyses. Where *Idhp-1* was not seen in the phenotype of a population, it was scored as being homozygous null (with a dummy allelic designation in BIOSYS-1) for the purposes of distance calculations.

Results

The electrophoretic results are presented in Tables 1 and 2. Table 1 shows the number of individuals scored from each population of the species described herein and from *Caledoniscincus orestes*. In both Tables 1 and 2 *C. austrocaledonicus* and *C. haplorhinus* are each represented by pooled populations. A more detailed account of variation in *C. austrocaledonicus* will be presented elsewhere. The names of the scored enzymes, together with abbreviations and Enzyme Commission Numbers are also listed in Table 1, and a matrix of genetic distances between *Caledoniscincus* populations is given in Table 2. A UPGMA dendrogram of genetic distances between populations is shown in Figure 1. Eight groups can be clearly distinguished. The Nei Unbiased distance between any pair of populations from different groups is at least 0.25.

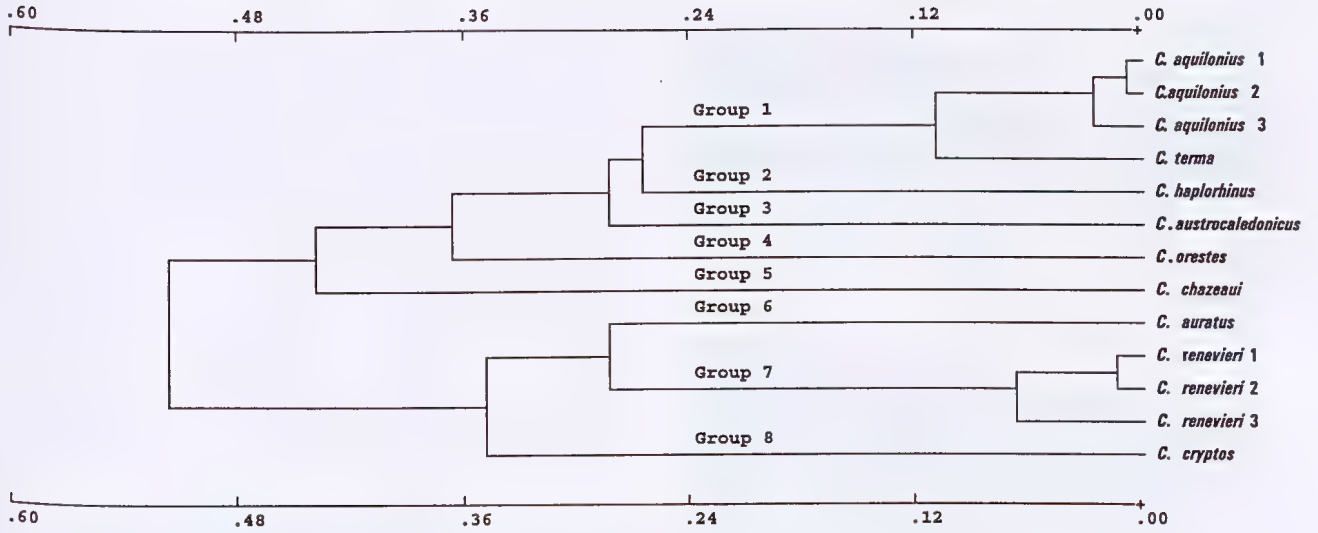

Figure 1. UPGMA dendrogram of relationships between *Caledoniscincus* populations based on Nei's unbiased genetic distance. Population names are the same as in Table 1.

Group 1 includes 4 populations from the far north of the island separated from group 2, the next most genetically similar group, by a Nei unbiased genetic distance of 0.27. Within group 1 are two subgroups (with a Nei unbiased genetic distance of 0.10) that are here described as two species on the basis of consistent morphological differences (coloration, scalation, osteology) between the type populations of each species. The first species, *Caledoniscincus aquilonius*, is represented in the genetic study by three populations, one from Koumac (*C. aquilonius* 1), one from Mt Panié (*C. aquilonius* 2) here designated as the type population, and the third from Kavaatch (*C. aquilonius* 3); the second species, *Caledoniscincus terma*, consists of a single population from Mt Mandjélia.

Groups 2 and 3 comprise those populations formerly assigned to *Caledoniscincus austrocaledonicus*. Our studies show *C. austrocaledonicus* to be a single widespread species that exhibits marked dimorphism in colour and pattern between northern and southern populations. A second widespread species, *Caledoniscincus haplorhinus*, occurs in open coastal and near coastal habitats, mainly on the west coast of the island, but also at scattered localities on the east coast and in the Loyalty Islands. *Caledoniscincus haplorhinus* is similar in size and appearance to *Caledoniscincus austrocaledonicus* from the north and central regions of the island, most notably in also having a white midlateral stripe. Both species are regionally and often locally sympatric along the west coast. The formal recognition of these genetic groups as distinct species is supported by differences in adult male ventral coloration and the positioning and delineation of the white midlateral stripe.

Group 2 represents *Caledoniscincus haplorhinus* (5 populations pooled—all from the west coast of the island).

Group 3 represents *Caledoniscincus austrocaledonicus* s.str. (20 populations pooled) as defined above.

Group 4 represents *Caledoniscincus orestes* from Mt Panié on the northeast ranges as defined by Sadlier (1986).

Groups 5, 6, and 7 are recognised as distinct species on the basis of a combination of scalation and electrophoretic criteria, while group 8 (a single adult male) is currently recognised solely on electrophoretic criteria.

Group 5 (*Caledoniscincus chazeaui*) represents a population from closed forest in the area of limestone rock outcropping on the northeast coast near Hienghène. Group 5 is separated from groups 1 to 4 by a Nei unbiased distance of 0.44.

Groups 6–8 form a discrete cluster separated from groups 1–5 by a Nei unbiased distance of 0.51.

Group 6 (*Caledoniscincus auratus*) consists of a single population from Koumac (where it is sympatric with *C. aquilonius* 2) on the northwest coast. Group 6 is separated from group 7, the next most genetically similar group, by a Nei unbiased distance of 0.28

Group 7 (*Caledoniscincus renevieri*) comprises three populations in the central ranges of the island: Mt Aoupinié (*C. renevieri* 1), Grottes des Adio (*C. renevieri* 2), and Col des Roussettes (*C. renevieri* 3).

Group 8 (*Caledoniscincus cryptos*), represented by a single individual from near Col d'Amieu in the central ranges, is separated from those populations in the group 6 + 7, the next most genetically similar group, by a Nei unbiased distance of 0.35.

Whilst genetic distances give a general idea of a population's affinities, inspection of the allozymic frequency data is required for a clearer picture. Notably, each of the groups defined above (except groups 1 and 6) are fixed, for at least one locus, for an allozyme which is seen nowhere else in the data. For Group 2 (*C. haplorhinus*) such allozymes are found at both *Idhp-1* and *Idhp-2*; for Group 3 (*C. austrocaledonicus*) at *Aat-1*, for Group 4 (*C. orestes*) at *Fh-2* and *Idhp-2*, for Group 5 (*C. chazeaui*) at *Aat-1*, for Group 7 (*C. renevieri*) at *Idhp-1*, and for Group 8 (*C. cryptos*) at *Gapdh*. Inspection of the data in Table 1 reveals sufficient fixed differences ("fds") between groups (with the possible exception of *C. aquilonius* and *C. terma*)

to support all of the taxonomic decisions made below. For instance, *C. aquilonius* and *C. terma* are differentiated from Group 2 by fds at *Gpd, Idhp-1, Idhp-2* and (nearly fixed) *Pgm. Caledoniscincus renevieri* and *C. auratus* are differentiated by fds at *Idhp-1, Pep:LA, Pep:LGG* and *Pgdh. Caledoniscincus cryptos* is distinguished from both of these species by fds at *Fbp, Gapdh* and *Gpd*. There are two fds between the morphospecies *C. aquilonius* and *C. terma* (*Idhp-2* and *Pgdh*) and the GPI C allozyme which is common, but not abundant, in the former is apparently absent from the latter.

Species descriptions

The species dealt with in this paper are small to moderately large in size, with well-developed limbs and digits, long tails, an obvious ear opening, and share the following basic suite of scalation characters: frontonasal broader than long; prefrontals when present moderately large and widely separated; frontal almost as broad as long; supraoculars four; frontoparietals fused; interparietal distinct; parietal bordered by a nuchal and upper secondary temporal; primary temporal single; upper and lower secondary temporals single; tertiary temporals two; postlabials two; nasals moderately to widely separated; loreals two, in a horizontal sequence; upper and lower preocular present; supraciliaries usually 7; upper labials usually 7; lower labials 6; postmental contacting first and second lower labials; enlarged chinshields three, first pair in broad contact; lower eyelid with an obvious, centrally located semi-transparent disc; ear opening with enlarged auricular lobules anteriorly and numerous blunt conical scales around the upper, lower, and posterior edges; body scales of dorsal and lateral surfaces tricarinate, each keel usually interrupting the posterior scale edge, number of keels on dorsal scales increasing towards nape. All species also have 29 presacral vertebrae (occasionally 28 or 30) and a phalangeal formula for the manus and pes of 2.3.4.5.3 and 2.3.4.5.4 respectively.

The species accounts below describe variation in proportions, and certain features of scalation, osteology, and coloration for each species, and report on their distribution and habits.

Caledoniscincus austrocaledonicus (Bavay)

Figs. 2, 3

Lygosoma austro-caledonica Bavay, 1869: 21.
Lygosoma austro-caledonicum dorsovittatum Roux, 1913: 118.
Leiolopisma dorsovittatum bodoi Borner, 1980: 8.

Problems in resolving the taxonomy of *Caledoniscincus austrocaledonicus* stem from the sexual and regional variability in coloration in this species, its occurrence in the north of the island with a closely related and morphologically very similar species, and the apparent loss of the specimens upon which the original description was based. The history of synonyms for this species are presented chronologically below.

The description of *Lygosoma austro-caledonica* by Bavay (1869) is composite (Sadlier, 1986) in that it identifies two forms. It was one of eight new scincid

Figure 2. *Caledoniscincus austrocaledonicus* male (upper) and female (lower) from Mt Aoupinié.

lizards described by him from New Caledonia for which no types were designated at the time of description, nor any indication as to where the specimens on which the descriptions were based were lodged.

The species *Euprepes haplorhinus* described by Günther (1872) from the Fiji Islands was placed in the synonymy of *L. austro-caledonicum* by Boulenger (1887) and the locality of "Fiji" was indicated as being in error for New Caledonia.

The first major revision of the New Caledonian herpetofauna was by Roux in 1913, based mainly on collections made by Roux and Sarasin in New Caledonia in 1911. Roux recognised four subspecies in *Lygosoma austro-caledonicum*. In addition to the nominate form, Roux described three new subspecies: *Lygosoma austro-caledonicum dorsovittatum*; *Lygosoma austro-caledonicum atropunctatum*; and *Lygosoma austro-caledonicum festivum*. Roux considered *Lygosoma austro-caledonicum atropunctatum* represented one of the forms of *Lygosoma austro-caledonica* described by Bavay (1869), and *Euprepes haplorhinus* Günther (1872) a synonym of *Lygosoma austro-caledonicum*. Kramer (1979) subsequently designated lectotypes for all Roux's subspecies of *Lygosoma austro-caledonicum*.

Borner (1980) described the subspecies *Leiolopisma dorsovittatum bodoi* from the Ile des Pins.

Brygoo (1985) published a catalogue of scincid types in the Paris Museum which included a number of Bavay type specimens that had until that time been regarded as lost (Sadlier, 1986). However the types of *Lygosoma austro-caledonicum* Bavay were not among those listed.

Sadlier (1986) reviewed the taxonomy of *Caledoniscincus* and proposed a neotype for *Lygosoma austro-caledonicum* Bavay, an adult female from Mt Aoupinié in the central ranges. In colour and pattern this specimen is typical of females found in populations occurring in the central and northern ranges and coast of New Caledonia. Roux's subspecies *Lygosoma austro-caledonicum atropunctatum* and *Lygosoma austro-caledonicum festivum* were recognised as distinct species by Sadlier (1986), and *Euprepes haplorhinus* Günther, *Lygosoma austro-caledonicum dorsovittatum* Roux, and *Leiolopisma dorsovittatum bodoi* Borner were all placed in the synonymy of *C. austrocaledonicus*.

The research presented here clearly identifies *Lygosoma austro-caledonicum* Bavay and *Euprepes haplorhinus* Günther as distinct species. *Lygosoma austro-caledonicum dorsovittatum* Roux and *Leiolopisma dorsovittatum bodoi* Borner are regarded here as conspecific with *Lygosoma austro-caledonicum* Bavay.

Material examined. All from Mt Aoupinié as follows: AMS R77643–45, R77649 forestry camp, 21°09'S 165°20'E; R77690, R77692 2 km NE of Mt Aoupinié forestry camp by road, 21°08'S 165°21'E; R77707, R77710–14, R146369 creek crossing 1 km NE of forestry camp by road, 21°08'S 165°20'E; R77739–40, R77755–56, R146379 summit, 21°11'S 165°16'E; R77757 (NEOTYPE), R77758 4 km from summit by road, 21°11'S 165°16'E; R77759–61 6 km from summit by road, 21°11'S 165°16'E; R146376–77 creek 1.3 km below logging camp, 21°08'S 165°20'E; R146386 1.5–2.5 km below logging camp, 21°07'S 165°19'E.

Figure 3. Lateral view of *Caledoniscincus austrocaledonicus* (upper and middle) and *Caledoniscincus haplorhinus* (lower) showing positioning of pale midlateral stripe in region of ear opening.

Diagnosis. *Caledoniscincus austrocaledonicus* is a widespread and morphologically variable species that shows variation in coloration between sexes and between populations in the south and north of the main island. It can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size (39–57 mm SVL); (*b*) tail approximately 1.5 times longer than body; (*c*) midbody scales in 28–32 rows; (*d*) paravertebral scales in 56–65 rows; (*e*) postsacral vertebrae >46; (*f*) adult males with pale vertebral markings and usually a broad, pale dorsolateral margin; (*g*) lateral surface with (northern and central populations) or without (southern) a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak; (*i*) adult males with an orange flush to the ventral surface in life. Note that estimates of tail length and postsacral vertebrae number are derived from populations other than those represented in Table 3.

This combination of characters distinguishes *Caledoniscincus austrocaledonicus* from all other members of the genus with the exception of *C. haplorhinus*. *Caledoniscincus austrocaledonicus* from the northern and central regions of the island are very similar in size, scalation, and certain aspects of coloration to *C.*

haplorhinus, most notably in also having a pale midlateral stripe. However, in *C. austrocaledonicus* from the northern and central regions of the island this stripe is usually poorly defined or obscure in the area between the forelimbs and ear opening (Fig. 3), and when obvious anteriorly this stripe meets the ear opening at the posteromedial edge. In contrast, the pale midlateral stripe in *C. haplorhinus* is usually well defined along its entire length and meets the ear at the upper or posteromedial edge of the ear and extends forward to form a pale edging over the ear (Fig. 3). The ventral colour in life of adult male *C. austrocaledonicus* is usually orange whereas adult male *C. haplorhinus* usually have yellow venters. *Caledoniscincus terma* is similar to *C. austrocaledonicus* from the southern regions of the island in having pale vertebral markings and no pale midlateral stripe. However, *C. austrocaledonicus* from this region have a longer tail (>45 *vs* 35–38 postsacral vertebrae or a tail length of ≈150 *vs* 130–140% SVL) than *C. terma*, and the ventral colour in life of adult male *C. austrocaledonicus* is usually orange *vs* usually yellow in adult male *C. terma*.

Description. It is beyond the scope of this study to analyse inter and intra population variation in scalation or osteology in *C. austrocaledonicus*. The data presented in the following description is based on 28 specimens (16 males and 12 females) from the neotype population (including the neotype) at Mt Aoupinié in the central ranges (*C. austrocaledonicus* [north] of Table 3).

Measurements: adult size 44–57 mm SVL; distance from axilla to groin 52.9–61.4% of SVL ($\bar{x}$ = 56.6, n = 28); distance from forelimb to snout 33.3–41.3% of SVL ($\bar{x}$ = 37.7, n = 28); hindlimb length 33.3–46.8% of SVL ($\bar{x}$ = 41.2, n = 28); tail length approximately 150% of SVL estimated from individual with most complete tail.

Scalation. midbody scales in 30–32 rows ($\bar{x}$ = 31.2, SD = 0.99, n = 28); paravertebral scales in 58–65 rows ($\bar{x}$ = 61.2, SD = 1.84, n = 28), no significant variation (P value ≤0.05) between males and females ($\bar{x}$ = 61.2 *vs* 61.3, t_{26} = -0.204, P = 0.840); dorsal scales of fourth finger 11–12 ($\bar{x}$ = 11.3, SD = 0.40, n = 28); lamellae of fourth finger 15–18 ($\bar{x}$ = 16.5, SD = 0.69, n = 28); dorsal scales of fourth toe 16–19 ($\bar{x}$ = 17.0, SD = 0.56, n = 28); lamellae of fourth toe 26–33 ($\bar{x}$ = 28.7, SD = 1.74, n = 28).

Osteology. Presacral vertebrae 29 (n = 15), rarely 28 (n = 1); no specimens with complete, original tails in sample to assess postsacral vertebrae number but specimen with most complete original tail has >50 postsacral vertebrae.

Coloration. *Caledoniscincus austrocaledonicus* shows marked sexual dimorphism in base colour of the dorsal and lateral surfaces. In males the dorsal and lateral colour is similar and the ventral surface usually red-orange. In females the dorsal surface is lighter than the lateral surface i.e. markedly two-toned, and the ventral surface is usually yellow. Juveniles and subadults of both sexes have the colour and pattern of adult females. The colour description below is based on specimens from the neotype locality at Mt. Aoupinié in the central ranges, but is broadly applicable to other populations of *C. austrocaledonicus* in the central and northern regions of the island.

Males: dorsal surface of body mid to dark brown with numerous pale flecks and distinctive pale vertebral markings, grey-brown in colour, rough-edged, and extending variably from nape to mid-dorsum as a stripe (≈1 scale wide) before breaking into a series of poorly connected elongate blotches over posterior half of body; head lighter than dorsum, with a coppery flush and dark longitudinal streak on rostrum. Dorsolateral margin pale (usually colour same as pale vertebral markings), moderately broad (≈1–1.5 scales wide), and forming a conspicuous rough-edged stripe from rostral to and along the basal portion of tail, distinct from both dark dorsal and upper lateral colour. Lateral surface mid-dark brown and with a pale midlateral stripe; upper lateral surface similar to dark dorsal colour but darker than lower lateral surface; pale midlateral stripe rough-edged and extending from level of ear opening to base of hindlimb (sometimes broken by an extension of dark brown colour of forelimb onto adjacent lateral surface), usually poorly defined or obscure in area between forelimbs and ear opening, when obvious anteriorly pale midlateral stripe meets ear opening at posteromedial edge; area above and in front of ear opening same as adjacent lateral surface, occasionally with numerous white markings which coalesce around upper edge of ear opening (resembling the extension of pale midlateral stripe characteristic of *C. haplorhinus* but not as well defined or complete). Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs orange, continuing variably along underside of tail.

Females: dorsal surface light to mid brown; laterodorsal margin (scale row 3) with dark markings to every second or third scale to give appearance of a longitudinal series of dark flecks, dorsolateral edge distinct, variably with a pale (lighter than adjacent dorsal colour), narrow (less than a scale width), margin. Lateral surface mid-dark brown (contrasting markedly with adjacent dorsal surface) and with a pale midlateral stripe; upper lateral surface darker than lower; pale midlateral stripe clean-edged and extending from level of ear opening to base of hindlimb, definition of pale midlateral stripe as for males (above). Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs yellow, continuing variably along underside of tail.

Variation. Data in Table 3 indicate populations of *Caledoniscincus austrocaledonicus* from the south of the species range tend to be smaller in size, have fewer midbody scale rows and paravertebral scales, and in coloration lack a pale midlateral stripe.

Regional differences in the presence or absence of a pale midlateral stripe in *Caledoniscincus austrocaledonicus* have confused previous taxonomies. Populations which share the coloration characteristics of the neotype (a well-developed midlateral stripe) extend throughout the central and northern regions of the island, the southernmost populations occurring at Voh on the west coast, Col des Roussettes in the central mountain chain, and Houaïlou on the east coast. In the central mountain chain populations immediately south of Col des Roussettes have this coloration characteristic poorly expressed (males lack a pale midlateral stripe but some females have a poorly defined stripe), and those that occur in the south of the island (this is the area at and south of the northern limit of the extensive southern ultramafic

region), the Ile des Pins, and the Loyalty Islands do not have this coloration characteristic.

Details of neotype. Adult female; size 53 mm SVL; distance from axilla to groin 32 mm; distance from forelimb to snout 19 mm; hindlimb length 19 mm; tail length 66 mm, regenerated.

Midbody scales rows 30; paravertebral scale rows 59; dorsal scales of fourth finger 11/12; lamellae of fourth finger 16/16; dorsal scales of fourth toe 16/16; lamellae of fourth toe 27/27.

Distribution. The species is widespread throughout New Caledonia and the islands of the region including the Ile des Pins, and Ouvéa, Lifou, and Maré in the Loyalty Islands group.

Biology. *Caledoniscincus austrocaledonicus* occurs throughout a wide range of forest and shrubland habitats across a broad altitudinal range. It is most commonly observed at the forest edge or in sunlit patches on the forest floor, but also occurs in coastal scrubs and maquis shrubland habitat. It is sympatric with *C. haplorhinus* at various lowland localities in both the north and south of New Caledonia and the islands of the region. In the north of the island the two species are sympatric at several mid-high altitude locations. Where the two species do occur at the same location, *C. austrocaledonicus* inhabits the forest edge and open areas of the forest interior, whereas *C. haplorhinus* occurs in more open adjacent habitat and tends to be extralimital at the forest edge. In such situations both species are syntopic at the forest edge.

Comments. The description of *Caledoniscincus austrocaledonicus* by Sadlier (1986) was composite and contained specimens of *C. haplorhinus*.

Other material examined. With the exception of tail length and postsacral vertebrae the values presented in Table 3 for *C. austrocaledonicus* from the south of the island (austro sth.) are taken from the following material: AMS R77442–43, R77445, R77448, R78309, R78311–12, R78315, R78324 Nouméa, Fambourg Blanchot (rue de Capitain Ferraud), 20°18'S 166°27'E; R77470 Nouméa, Mont-Coffyn, 20°18'S 166°27'E. Values for tail length and postsacral vertebrae presented in Table 3 are taken from a sample of two specimens from Plateau de Dogny.

Caledoniscincus haplorhinus Günther

Figs. 3, 4

Euprepes haplorhinus Günther, 1872: 419.

Type material. HOLOTYPE: BMNH 1946.8.13.45.

Material examined. AMS R77407, R77409, R77427, R77437, R77449–52, R 78319–20, R78322, R78326–28 Nouméa, Fambourg Blanchot, 20°18'S 166°27'E; AMS R135119–23 Isle Nou, vicinity Nouville, 22°16'S 166°24'E; AMS R146433–43, CAS 198763–71 Plage de Ouano, 21°50'S 165°48'E; AMS R144257–58, R144284–93 Koumac Caves, approx. 9 km E of Koumac, 20°33'S 164°21'E; AMS R146459–72 Pindaï, Plage de Pindaï, 21°21'S 164°57'E.

Diagnosis. *Caledoniscincus haplorhinus* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size (42–55 mm SVL); (*b*) tail approximately 1.65 times longer than body; (*c*) midbody scales in 28–32 rows; (*d*) paravertebral scales in 59–67 rows; (*e*) postsacral vertebrae >50; (*f*) adult males with pale vertebral markings and broad pale dorsolateral margin; (*g*) lateral surface with a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak; (*i*) adult males with a yellow flush to ventral surface in life.

Description. the description is based on 61 specimens (51 adults and 10 subadults) and includes samples from four (Isle Nou, Plage de Ouano, Koumac Caves and Pindaï) of the five populations used in the electrophoretic study.

Measurements. Maximum adult size 55 mm SVL; distance from axilla to groin 51.0–63.3% of SVL ($\bar{x}$ = 57.0, n = 50); distance from forelimb to snout 34.7–40.4% of SVL ($\bar{x}$ = 37.6, n = 50); hindlimb length 33.3–42.5% of SVL ($\bar{x}$ = 38.8, n = 49); tail length 156.0–173.5% of SVL ($\bar{x}$ = 165.1, n = 4—note this includes 3 adults with nearly complete tail only).

Scalation. Midbody scales in 28–32 rows ($\bar{x}$ = 30.0, SD = 1.06, n = 61); paravertebral scales in 59–67 rows ($\bar{x}$ = 63.0, SD = 1.63, n = 61) significant variation (P value ≤0.05) between males and females ($\bar{x}$ = 62.5 *vs* 63.5, t_{49} = -2.535, P = 0.014); dorsal scales of fourth finger 10–12 ($\bar{x}$ = 10.9, SD = 0.62, n = 60); lamellae of fourth finger 14–18 ($\bar{x}$ = 15.8, SD = 0.67, n = 60); dorsal scales of fourth toe 14–18 ($\bar{x}$ = 16.6, SD = 0.91, n = 60); lamellae of fourth toe 25–31 ($\bar{x}$ = 28.0, SD = 1.38, n = 60).

Osteology. Presacral vertebrae 29 (n = 12); postsacral vertebrae 51 (n = 2) to 55 (n = 1).

Coloration. Males: dorsal surface mid to dark brown with numerous pale flecks and distinct pale vertebral markings, grey-brown in colour, rough-edged, and extending from nape to mid-dorsum as a stripe before breaking into a series of poorly connected elongate blotches over posterior half of body; head lighter than dorsum, with a coppery flush and dark longitudinal streak on rostrum. Dorsolateral margin pale (grey-brown similar to pale vertebral markings), moderately broad (≈1–1.5 scales wide), and forming a conspicuous rough-edged stripe from rostral to and along basal portion of tail, distinct from both dark dorsal and upper lateral colour. Lateral surface mid-dark brown and with a pale midlateral stripe, upper lateral surface darker than lower lateral surface (darker than or similar to dorsal colour); pale midlateral stripe (usually dark edged) well defined along its entire length and extending from level of ear opening to base of hindlimb, meeting ear at upper or posteromedial edge and extending forward to form a pale edging over the ear. Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs with a yellow flush, continuing variably along underside of tail.

Females: dorsal surface light to mid brown, occasionally grey, uniform or with variably distinct pale vertebral

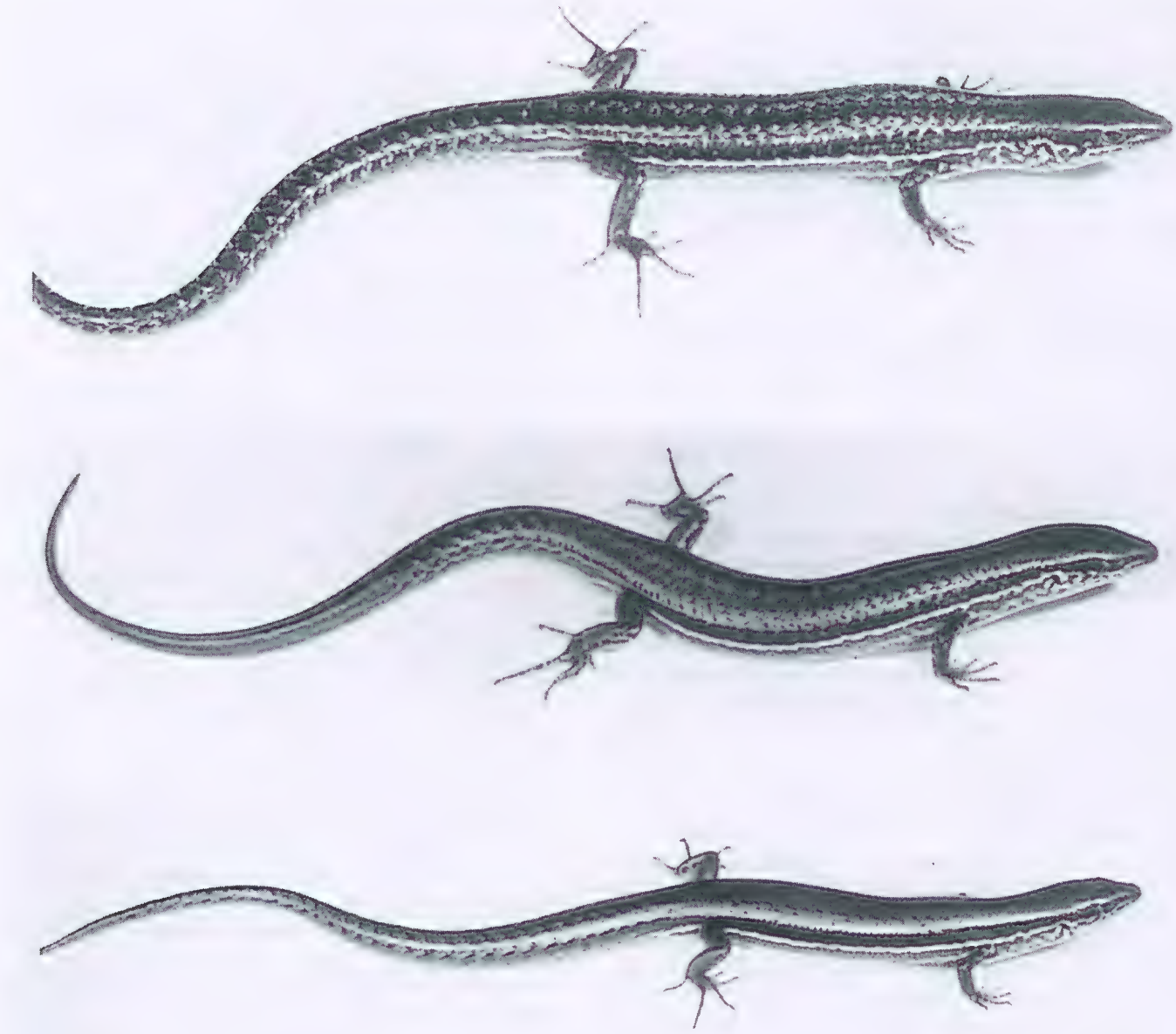

Figure 4. *Caledoniscincus haplorhinus* males from Pindaï (upper) and Koumac (middle), and female from Koumac (lower).

markings, grey-brown in colour, and extending from nape to mid-dorsum as a stripe before breaking into a series of poorly connected elongate blotches over posterior half of the body. Lateral surface mid-dark brown (darker than and contrasting markedly with adjacent dorsal colour) with a pale midlateral stripe, upper lateral surface darker than lower lateral surface; pale (dark edged) midlateral stripe clean-edged, extending from level of ear opening to base of hindlimb, and positioned to meet ear as described for males. Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs pale yellow, continuing variably along underside of tail.

Juveniles and subadults of both sexes have coloration of adult females, and dorsal and lateral surfaces and pale midlateral stripe well defined.

Variation. Samples of both sexes from beachfront locations can be paler overall in coloration, grey replacing brown as the background tone. In some adults from these locations the definition of the pale midlateral stripe is poor anteriorly and its position relative to the ear opening difficult to assess.

Details of holotype. Adult male; size 50 mm SVL; distance from axilla to groin 28 mm; distance from forelimb to snout 19 mm; hindlimb length 21 mm; tail length 64 mm, regenerated.

Midbody scales rows 28; paravertebral scale rows 62; dorsal scales of fourth finger 11/11; lamellae of fourth finger 17/17; dorsal scales of fourth toe 17/17; lamellae of fourth toe 29/28.

Distribution. Widespread in coastal and near coastal areas of the west coast of New Caledonia, and scattered locations on the east coast from near Ouaïème in the north to Houaïlou midway along the coast. Also recorded from two mid altitude sites (≈500 m asl) and one high altitude site (≈1,000 m asl on Mt Ignambi) in the northeast ranges. Widespread throughout the islands of the region including the Ile des Pins off southern New Caledonia, Ouvéa, Lifou, and Maré Islands of the Loyalty Islands group, and Ile Surprise off northern New Caledonia.

Biology. Occurs in open coastal and near coastal habitats including grassed, beachfront sand-dunes, edges of forest habitat, and disturbed areas such as plantations and urban gardens.

Caledoniscincus haplorhinus is sympatric with *C. austrocaledonicus* at a number of coastal and lowland localities throughout the main island of New Caledonia, and the islands of the region (see comments the account of *C. austrocaledonicus* above).

Gravid females from Plage de Ouano collected in January 1995 had 3 (1/2, n = 4, SVL 42–48 mm) and 5 (2/3, n = 1, size not determined) enlarged yolked ovarian follicles, and specimens from Nouméa collected in March 1990 had 2 (1/1, n = 2, 43–47 mm) shelled oviducal eggs.

Comments. The description of *Caledoniscincus austrocaledonicus* by Sadlier was composite and contained specimens of *C. haplorhinus* (see comments the account of *C. austrocaledonicus* above). Specimens refereed to as *C. austrocaledonicus* from Isle Surprise (Bauer *et al.*, 1992) are *C. haplorhinus*.

Caledoniscincus aquilonius n.sp.

Figs. 5, 6

Type material. HOLOTYPE: AMS R144200 Mt Panié, New Caledonia, 20°33'27"S 164°47'15"E (R. Sadlier, 20.viii.1994). PARATYPES: AMS R144198–204, R144206–13, R144227–28, CAS 203480–82, MNHN 1997.3331-32 same location as holotype.

Etymology. The species name is from the Latin *aquilonius*, meaning northern, alluding to the distribution of this species in the north of New Caledonia.

Diagnosis. *Caledoniscincus aquilonius* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size (39–49 mm SVL); (*b*) tail (average) approximately 1.5 times longer than body; (*c*) midbody scales in 30–34 rows; (*d*) paravertebral scales in 54–58 rows; (*e*) postsacral vertebrae 40–44; (*f*) adult males with a broad pale laterodorsal margin and dorsal pattern of scattered light flecks; (*g*) lateral surface without a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak; (*i*) adult males with an orange flush to the ventral surface in life.

Description. The description is based on a series of 15 specimens (8 males and 7 females) collected at the type location, and includes specimens used in the electrophoretic study.

Measurements. Adult size 39–49 mm SVL; distance from axilla to groin 52.2–59.2% of SVL ($\bar{x}$ = 56.2, n = 15); distance from forelimb to snout 36.7–41.3% of SVL ($\bar{x}$ = 39.2, n = 15); hindlimb length 32.7–40.9% of SVL ($\bar{x}$ = 37.3, n = 12); tail length 146.3–162.8% of SVL ($\bar{x}$ = 154.6, n = 2).

Scalation. Midbody scales in 30–34 rows ($\bar{x}$ = 32.2, SD = 1.08, n = 15); paravertebral scales in 54–58 rows ($\bar{x}$ = 55.8, SD = 1.65, n = 15), no significant variation (P value ≤0.05) between males and females ($\bar{x}$ = 55.3, n = 8 *vs* 56.4, n = 7, t_{13} = -1.425, P = 0.178); dorsal scales of fourth finger 9–10 ($\bar{x}$ = 9.6, SD = 0.46, n = 15); lamellae of fourth finger 13–16 ($\bar{x}$ = 14.4, SD = 0.73, n = 14); dorsal scales of fourth toe 11–14 ($\bar{x}$ = 13.0, SD = 0.34, n = 14); lamellae of fourth toe 23–27 ($\bar{x}$ = 25.2, SD = 1.14, n = 14).

Osteology. Presacral vertebrae 29–30 ($\bar{x}$ = 29.1, SD = 0.26, n = 15); postsacral vertebrae 43–44 (n = 2).

Coloration. Males: dorsal surface variable, background colour ranging from mid brown with numerous pale flecks to more or less uniformly dark brown; pale markings boldest anteriorly around region either side of forelimb and comprising a dark-edged cream fleck on every third longitudinal scale row forming a rough, transversely aligned, pale bar; dorsolateral region grey to pale brown (sometimes darker) with dark flecks, and forming a broad (usually 2 scales wide) and conspicuous pale, rough-edged stripe from rostral to basal portion of the tail. Lateral surface lighter in tone than dorsal, mid-dark brown uppermost with similar pale and dark spotting as dorsal surface, becoming paler towards venter and suffused with orange ventral colour. Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs orange, continuing variably along underside of tail. Throat grey when viewed obliquely but with a faint orange wash when viewed ventrally.

Females: dorsal surface mid to dark brown with occasional fine dark spotting, particularly towards nape; scales on vertebral axis slightly lighter in colour in some individuals and giving the appearance of a faint, pale stripe down the centre of back; head lighter in colour than adjacent dorsal surface. Lateral surface dark brown to black (darker than dorsal surface) becoming paler towards the venter, unmarked or with a few scattered dark markings uppermost, and in larger individuals with a well defined pale dorsolateral margin (≈1.5 scales wide). Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs orange, continuing variably along underside of tail. Throat with numerous fine dark specks along the posterior edge of each scale giving an overall grey appearance but with a faint orange wash when viewed ventrally.

Details of holotype. Adult male; SVL 44 mm; distance from axilla to groin 25 mm; distance from forelimb to snout 18 mm; hindlimb length 18 mm; tail length 56 mm, reproduced.

Figure 5. Distribution of six new species of Caledoniscincus in New Caledonia as follows: *Caledoniscincus aquilonius* (O type locality = 1), *Caledoniscincus terma* (◆ type locality = 2), *Caledoniscincus renevieri* (● type locality = 3), *Caledoniscincus auratus* (▲ type locality = 4), *Caledoniscincus chazeaui* (* type locality = 5), and *Caledoniscincus cryptos* (❐ type locality = 6).

Midbody scales rows 32; paravertebral scale rows 56; dorsal scales of fourth finger 10/10; lamellae of fourth finger 14/14; dorsal scales of fourth toe 13/13; lamellae of fourth toe 25/26.

Presacral vertebrae 29.

Distribution. The type series is restricted to Mt Panié in the northeast ranges of New Caledonia (Fig. 5). Samples assigned to this species but not included in the type series are known from several other locations in the northeast coast and ranges (Kavaatch in the Hienghène Valley; Ouinguip between Hienghène and the Ouaïème River; Tao near the base of Mt Panié; and upper reaches of the Hienghène Valley) and two extralimital localities, one at Koumac Caves on the northwest coast and one from the main range between Kone and Poindimié. *Caledoniscincus aquilonius* is probably widespread in closed forest habitat in the north of the island.

Biology. Occurs in closed low-mid altitude forest, from near sea level at Tao to 690 m asl on Mt Panié.

Clutch size 3, gravid females (SVL 47 and 48 mm) collected during the summer wet season (January) contained oviducal eggs (1/2, n = 2).

Comments. The type series is restricted to the sample of specimens from Mt Panié which unambiguously represented a single species based on the genetic and morphological data are available. In both the Kavaatch and Koumac samples polymorphic allele's with no evidence of

Figure 6. *Caledoniscincus aquilonius* male (upper) and female (lower) from Mt Panié.

heterozygotes for the *Gpi* locus were present. While some specimens from each of these samples are regarded as conspecific with the type series, the genetic variation observed in the remaining specimens could be due to the presence of a second cryptic species. For this reason the Kavaatch and Koumac samples are not included in the type series. Several other samples are also here regarded as conspecific with *C. aquilonius* but were collected subsequent to the electrophoretic study and lack genetic data for inclusion in the type series. These samples represent populations from: the upper reaches of the Hienghène Valley; the Roches d'Ouaïème near Ouinguip; and main range between Kone and Poindimié.

The sample from Koumac Caves on the northwest coast (eight specimens included in the electrophoretic study) showed no significant differences in scalation to the type series of *C. aquilonius* from the northeast ranges. Variation in colour and pattern of adult male *C. aquilonius* from Koumac is however more difficult to assess as only a single subadult and single adult male were collected.

Two collections made in the northeast of the island from the upper reaches of the Hienghène Valley and Roches d'Ouaïème between Hienghène and the Ouaïème River were made subsequent to the electrophoretic analysis. These specimens fall within the range of variation in scalation for *C. aquilonius*, and most adult males have the broad pale laterodorsal margin typical of this species; hence they are here assigned to *C. aquilonius*.

A collection of specimens made at mid-altitude on the main range between Kone and Poindimié, is most similar to *C. aquilonius* but differs in having generally fewer midbody scale rows ($\bar{x} = 30$ *vs* 32) than the type series and the dorsolateral margin variably patterned. The dorsal coloration of the majority of adult males from this population is uniformly mid to dark brown with numerous, fine, pale and dark flecks, only a few individuals having what could be interpreted as a pale dorsolateral margin.

Two adult male *Caledoniscincus* from Mt Ignambi approximately 20 km north of Mt Panié (NHMB 7325 collected by Roux and Sarasin in 1911 and a single recently collected specimen AMS R152223) are similar in colour and pattern to *C. aquilonius* from Mt Panié, but differ in being larger (52–55 mm SVL), having more dorsal scale rows (60), and coming from a much higher altitude (1,000 m *vs* maximum 690 m for *C. aquilonius* on Mt Panié). It is unclear whether these specimens represent another undescribed species or variation in both scalation and altitudinal limits not previously observed in *C. aquilonius*.

Additional material. The following specimens are also assigned to *C. aquilonius* but not included in the type series: AMS R77864, R77894, R144205, R144214–15, R144255–56, R146364–65, R149311–13, R149319–23, 149342–43, R149961–62, R149965, Mt Panié; CAS 182062, CAS 198713 Tao, 20°33'S 164°48'E; AMS R77809, R77812, R138513 R144249, R144252–53 Kavaatch Forestry Camp (abandoned), 20°42"S 164°50'E; AMS R144296–

97, R144259, R146338–341 Koumac Caves, approximately 9 km E of Koumac, 20°33'S 164°21'E; AMS R150706, R150709–20 39.6 km W of Hienghène on Ouyaguette road, 20.40'S 164.42'E; AMS R151346–47 vicinity of Ouinguip, 20°38'S 164°51'E; AMS R150672–83, R150691–92 47.2 km from Kone turnoff on road to east coast, 20°54'S 165°07'E.

Caledoniscincus terma n.sp.

Figs. 5, 7

Type material. HOLOTYPE: AMS R146320 Mt Mandjélia, 10.3 km E Tade River crossing, New Caledonia, 20°24'S 164°30'E (R. Sadlier and A. Bauer, 4.iii.1995). PARATYPES: AMS R146312–14, R146316–19, R146321 same location as holotype; AMS R146344–46, MNHP 1997.3329 (formerly AMS R146315) Mt Mandjélia, 15 m asl below summit, 20°23'S 164°31'E 4/1/1995; MNHP 1997.3330 (formerly AMS R146348) Mt Mandjélia, 20°24'S 164°31'E.

Etymology. The species name is from the Latin *terma*, for end, alluding to the position of the type locality for this species at the northern end of the northeast ranges.

Diagnosis. *Caledoniscincus terma* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size 41–50 mm SVL; (*b*) tail relatively short, on average only 1.36 times longer than body; (*c*) midbody scales in 32–34 rows; (*d*) paravertebral scales in 55–63 rows; (*e*) postsacral vertebrae 37–38; (*f*) dorsal colour pattern of adult males featuring a pale vertebral stripe; lateral surface without a pale midlateral stripe; (*g*) rostral shield with a dark midrostral streak; (*h*) adult males with a yellow flush to the ventral surface in life.

Description. The description is based on a series of 14 specimens (4 males and 10 females) collected at the type location and includes specimens used in the electrophoresis study.

Measurements. Adult size 41–50 mm SVL; distance from axilla to groin 52.4–60.5% of SVL ($\bar{x}$ = 56.3, n = 14); distance from forelimb to snout 34.1–40.1% of SVL ($\bar{x}$ = 38.0, n = 14); hindlimb length 31.3–30.0% of SVL ($\bar{x}$ = 35.1, n = 14); tail length 131.1–140.5% of SVL ($\bar{x}$ = 135.8, n = 2).

Scalation. Midbody scales in 32–34 rows ($\bar{x}$ = 32.4, SD = 0.85, n = 14); paravertebral scales in 55–63 rows ($\bar{x}$ = 58.9, SD = 2.56, n = 14), no significant variation (P value ≤0.05) between males and females ($\bar{x}$ = 57.3, n = 4 *vs* 59.6, n = 10, t_{12} = -1.655, P = 0.124); dorsal scales of fourth finger 9–10 ($\bar{x}$ = 9.4, SD = 0.39, n = 14); lamellae of fourth finger 12–16 ($\bar{x}$ = 14.4, SD = 1.16, n = 14); dorsal scales of fourth toe 13–15 ($\bar{x}$ = 13.6, SD = 0.66, n = 14); lamellae of fourth toe 24–27 ($\bar{x}$ = 25.4, SD = 0.99, n = 14).

Osteology. Presacral vertebrae 29–30 ($\bar{x}$ = 29.1, SD = 0.26, n = 14); postsacral vertebrae 37–38 ($\bar{x}$ = 37.5, SD = 0.70, n = 2).

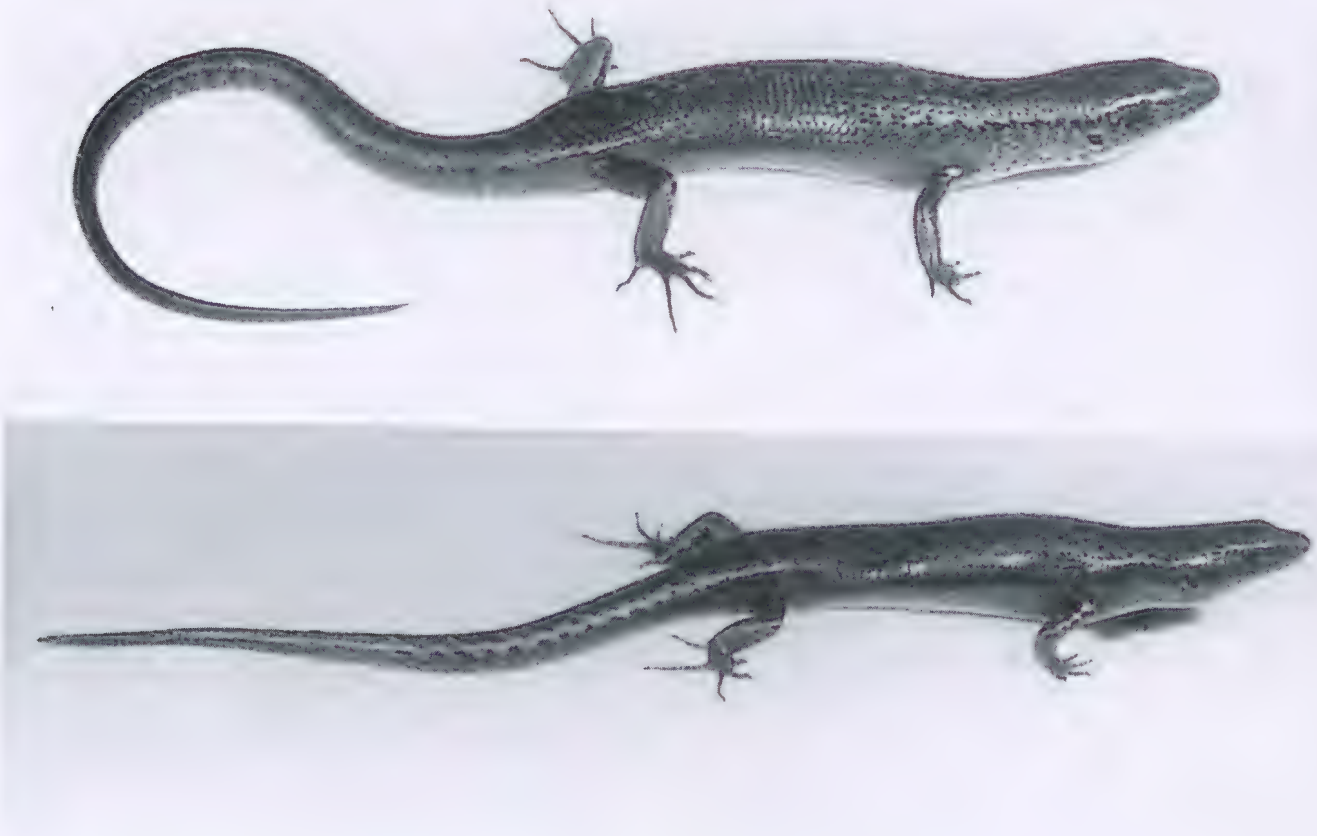

Figure 7. *Caledoniscincus terma* male (upper) and female (lower) from Mt Mandjélia.

Coloration. Males: dorsal surface dark brown and with scattered, pale, dark-edged flecks; vertebral axis with a pattern of pale grey blotches forming a near continuous rough-edged stripe. Lateral surface dark brown (similar in colour to dorsal surface) and differentiated from dorsal surface anteriorly by a row of black flecks along laterodorsal edge; dorsal and lateral colorations tend to merge posterior to forelimb, dorsolateral edge rough and poorly defined. Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs yellow, continuing variably along underside of tail.

Females: dorsal surface mid brown with occasional light and numerous scattered darker flecks, larger individuals (>47 mm SVL) with a variably present series of poorly differentiated pale grey blotches along vertebral axis forming an obscure, but near continuous, rough-edged stripe down centre of back. Lateral surface dark brown-black, unmarked and with a well defined dorsolateral margin. Ventral surface from level of forelimbs to basal portion of tail and underside of fore and hindlimbs usually orange, occasionally yellow.

Details of holotype. Adult male; SVL 44 mm; distance from axilla to groin 24 mm; distance from forelimb to snout 18 mm; hindlimb length 17 mm; tail length 67 mm, tip reproduced.

Midbody scales rows 34; paravertebral scale rows 58; dorsal scales of fourth finger 9/10; lamellae of fourth finger 14/14; dorsal scales of fourth toe 15/15; lamellae of fourth toe 26/25.

Presacral vertebrae 29.

Distribution. Known only from Mt Mandjélia, the northern most peak on the northeast ranges of New Caledonia (Fig. 5).

Biology. Restricted to mid (500 m) to high (760 m) altitude closed forest.

Clutch size 2–3, gravid females collected during the summer wet season (January) contained oviducal eggs (1/2, n = 2, SVL 40–46 mm and 1/1, n = 2, SVL 43–45 mm).

Additional material examined. The following specimens are assigned to *C. terma* but not included in the type series: AMS R135738–43, R135749–59, Mandjélia, at and near the summit, 20°24'S 164°32'E.

Caledoniscincus renevieri n.sp.

Figs. 5, 8

Type material. HOLOTYPE: AMS R146424 4.6 km N Col des Roussettes on Houaïlou-Bourail road, New Caledonia, 21°24'S 165°26'E (R. Sadlier and A. Bauer, 8.i.1997). PARATYPES: AMS R146392–95, R146423, R146425, R146427–29, CAS 198740–43, MNHP 19997.3333 (formerly AMS R146426), MNHP 1997.3334 (formerly AMS R146430) same data as holotype; AMS R135822 4.6 km N Col des Roussettes on Houaïlou-Bourail road, 21°24'S 165°26'E; AMS R77658–59, R77677 Mt Aoupinié (vicinity forestry camp 500 m), 21°09'S 165°20'E; AMS R146382–84 Mt Aoupinié (1.5–2.5 km below forestry camp), 21°07'S 165°19'E; AMS R146499–501 Grottes des Adio, NE of Poya, 21°15'S 165°14'E.

Etymology. The species is named for Alain Renevier of Nouméa in recognition the generous hospitality and support he and his family have given during our field research in New Caledonia.

Diagnosis. *Caledoniscincus renevieri* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size 37–51 mm SVL; (*b*) tail approximately 1.4 times longer than body; (*c*) midbody scales in 30–32 rows; (*d*) paravertebral scales in 51–58 rows; (*e*) postsacral vertebrae 41–44; (*f*) adult male dorsal colour pattern transversely oriented, occasionally with pale vertebral markings; (*g*) lateral surface without a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak; (*i*) adult males with a yellow flush to the ventral surface in life.

Description. The description is based on a series of 23 specimens (12 males and 11 females) collected at the type locations and includes specimens used in the electrophoresis study.

Measurements. Adult size 37–51 mm SVL; distance from axilla to groin 51.4–60.8% of SVL ($\bar{x}$ = 55.4, n = 23); distance from forelimb to snout 33.3–42.9% of SVL ($\bar{x}$ = 38.7, n = 23); hindlimb length 31.8–41.0% of SVL ($\bar{x}$ = 36.6, n = 23); tail length 127.3–154.3% of SVL ($\bar{x}$ = 140.2, n = 3).

Scalation. Midbody scales in 30–32 rows ($\bar{x}$ = 30.3, SD = 0.69, n = 23); paravertebral scales in 51–58 rows ($\bar{x}$ = 53.6, SD = 2.02, n = 23), significant variation (P value ≤0.05) between males and females ($\bar{x}$ = 52.4, n = 12 *vs* 54.9, n = 11, t_{21} = -3.730, P = 0.001); dorsal scales of fourth finger 8–10 ($\bar{x}$ = 9.0, SD = 0.49, n = 23); lamellae of fourth finger 13–16 ($\bar{x}$ = 13.6, SD = 0.61, n = 23); dorsal scales of fourth toe 12–13 ($\bar{x}$ = 12.7, SD = 0.47, n = 23); lamellae of fourth toe 21–29 ($\bar{x}$ = 24.7, SD = 1.40, n = 23).

Osteology. Presacral vertebrae 29–30 ($\bar{x}$ = 29.2, SD = 0.41, n = 20); postsacral vertebrae 41–44 ($\bar{x}$ = 42.7, SD = 1.53, n = 3).

Coloration. Males: dorsal surface light to mid brown with numerous pale, dark-edged flecks, dark edging of pale markings tending to align obliquely to form narrow, dark bars; pale markings along vertebral axis tending to align to form a near continuous rough-edged stripe in some larger individuals. Lateral surface darker than dorsal, variably with light and dark flecks; side of head and neck dark brown to black uppermost. Dorsolateral margin defined anteriorly (between eye and forelimbs) by a pale, narrow (<1 scale width), dark-edged stripe, becoming obscure between fore and hindlimbs. Ventral surface moderate to pale yellow in life posterior of forelimbs, throat with an orange tinge.

Females: dorsal surface light-mid brown, variably with scattered dark flecks. Lateral surface darker than dorsal; mid to dark brown uppermost and unmarked; side of head and neck dark brown-black uppermost in larger individuals (>47 mm SVL). Dorsolateral margin defined anteriorly

Figure 8. *Caledoniscincus renevieri* male (upper) and female (lower) from Col des Roussettes.

(between eye and forelimbs) by a pale, narrow (<1 scale width) stripe, contrasting markedly with dark upperlateral colour between eye and forelimbs, and by the contrasting dark lateral and light upper lateral colour between fore and hindlimbs. Ventral surface either without obvious ventral colour (AMS R146394–95, R146425–26) or with a very faint yellow (AMS R146428 and R146430) or pink (AMS R146384) flush.

Details of holotype. Adult male; size 46 mm SVL; distance from axilla to groin 24 mm; distance from forelimb to snout 18 mm; hindlimb length 18 mm; tail length 71 mm, complete.

Midbody scale rows 30; paravertebral scale rows 53; dorsal scales of fourth finger 9/9; lamellae of fourth finger 14/14; dorsal scales of fourth toe 13/13; lamellae of fourth toe 23/24.

Presacral vertebrae 29; postsacral vertebrae 41.

Distribution. Known from three locations in the central ranges at Mt Aoupinié and Grottes des Adio (western foothills of Mt Aoupinié) in the north to Col des Roussettes in the south (Fig. 5). All locations are in relatively close proximity to one another, the Adio and Mt Aoupinié locations are separated by 10 km, and these locations are approximately 25–30 km north of Col des Roussettes.

Biology. Lowland and mid-altitude closed forests where it can be relatively abundant. On Mt Aoupinié and at Col des Roussettes it was collected in closed forest gullies and at Adio Caves in closed forest at the base of limestone outcrops.

Clutch size 2–4 (mode 2), gravid females collected during the summer wet season (January) contained oviducal eggs (1/1, n = 5, SVL 41–47 mm; 1/2, n = 1, SVL 51 mm; and 2/2, n = 1, SVL 50 mm).

Caledoniscincus auratus n.sp.

Figs. 5, 9, 10

Type material. HOLOTYPE: AMS R144298 Koumac Caves, approximately 9 km E of Koumac, New Caledonia, 20°33'S 164°21'E (R. Sadlier, 23–24.iv.1994). PARATYPES: AMS R144299–300, R144304, MNHN 1997.3335 (formerly

Figure 9. *Caledoniscincus auratus* male from Koumac Caves.

AMS R144302), MNHN 1997.3336 (formerly AMS R144303) location as for holotype; AMS R144381–82 location as for holotype.

Etymology. The species name is from the Latin *auratus*, for golden or ornamented with gold, and alludes to the prominent gold flecking on adult males of this species.

Diagnosis. *Caledoniscincus auratus* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small size 38–51 mm SVL; (*b*) tail on average 1.47 times longer than body; (*c*) midbody scales in 28 rows; (*d*) paravertebral scales in 52–55 rows; (*e*) postsacral vertebrae 43–45; (*f*) adult male dorsal colour pattern transversely oriented and without a pale vertebral stripe; (*g*) lateral surface without a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak; (*i*) adult males with a yellow flush to the ventral surface in life.

Description. The description is based on specimens collected at the type locations and includes only those specimens used in the electrophoresis.

Measurements. Adult size 38–51 mm SVL; distance from axilla to groin 52.6–56.9% of SVL ($\bar{x}$ = 55.0, n = 8); distance from forelimb to snout 37.3–41.0% of SVL ($\bar{x}$ = 39.5, n =

Figure 10. Closed forest habitat at Koumac Caves, near type locality of *Caledoniscincus auratus*.

8); hindlimb length 31.4–39.5% of SVL ($\bar{x}$ = 37.5, n = 8); tail length 141.0–151.3% of SVL ($\bar{x}$ = 146.8, n = 4).

Scalation. Midbody scales in 28 rows (n = 8); paravertebral scales in 52–55 rows ($\bar{x}$ = 53.6, SD = 1.06, n = 8); dorsal scales of fourth finger 9–11 ($\bar{x}$ = 9.25, SD = 0.46, n = 8); lamellae of fourth finger 12–15 ($\bar{x}$ = 13.75, SD = 0.87, n = 8); dorsal scales of fourth toe 13–14 ($\bar{x}$ = 13.1, SD = 0.23, n = 8); lamellae of fourth toe 21–25 ($\bar{x}$ = 22.9, SD = 1.35, n = 8).

Osteology. Presacral vertebrae 29–30 ($\bar{x}$ = 29.2, SD = 0.41, n = 20); postsacral vertebrae 43–45 ($\bar{x}$ = 44.0, SD = 0.82, n = 4).

Coloration. Adult males: dorsal surface mid brown with a pattern of numerous pale, dark-edged spots, aligned to form a pattern of irregular and merging transverse bars (dark edging muted in smaller males 38–41 mm SVL); head with a few fine dark spots anteriorly. Lateral surface much lighter than dorsal, cream with a brownish wash uppermost and dark markings over most the surface; dark lateral markings largest and boldest uppermost, particularly in region between forelimb and ear opening, becoming suffused approaching the venter; laterodorsal margin between forelimb and ear opening light brown and distinct from darker lateral and dorsal colours. Ventral surface pale, with a moderate to dull yellow flush from level of forelimbs to basal portion of tail in some larger males.

Females: dorsal surface mid brown with sparse dark flecking. Lateral surface dark brown to black, uniform in colour; laterodorsal margin between forelimb and ear opening light brown and distinct from darker lateral and dorsal colours. Ventral surface pale, variably with a dull pink flush posterior of forelimbs in more mature females.

Details of holotype. Adult male; SVL 51 mm; distance from axilla to groin 29 mm; distance from forelimb to snout 19 mm; hindlimb length 16 mm; tail length 57 mm, mostly regenerated.

Midbody scales rows 28; paravertebral scale rows 52; dorsal scales of fourth finger 9/9; lamellae of fourth finger 13/14; dorsal scales of fourth toe 13/13; lamellae of fourth toe 24/24.

Presacral vertebrae 29.

Distribution. Known only from Koumac Caves in the northwest of New Caledonia (Fig. 5).

Biology. Restricted to lowland closed forest (Fig. 10), resembling dry monsoon forest, adjacent to limestone outcrops at Koumac Caves.

Additional material examined. The following specimens are assigned to *C. auratus* but not included in the type series. They agree with the types in morphology but were not part of the electrophoretic analyses: AMS R144301, R146331, R146333, R144384 same location as holotype.

Comments. A single female (SVL 43 mm) not included in the type series and collected during the summer wet season (January) had 3 oviducal eggs (1/2).

Caledoniscincus chazeaui n.sp.

Figs. 5, 11–13

Type material. HOLOTYPE: AMS R138515 Koulnoué, Hienghène region, New Caledonia, 20°41'32"S 164°59'10"E (R. Sadlier and A. Bauer, 26.ii.1992). PARATYPES: MNHP 1997.3337 (formerly AMS R138516), CAS 182073–74 same location as holotype.

Etymology. The species is named for Jean Chazeau of the Laboratoire de Zoologie Appliquée at ORSTOM Nouméa, in recognition of his generous support and enthusiasm for our research on New Caledonian lizards.

Diagnosis. *Caledoniscincus chazeaui* can be distinguished from the other species of *Caledoniscincus* by the following combination of characters: (*a*) small size 36–43 mm SVL; (*b*) tail approximately 1.36 times longer than body; (*c*) midbody scales in 28–30 rows; (*d*) paravertebral scales in 59–61 rows; (*e*) postsacral vertebrae 42; (*f*) adult dorsal colour pattern transversely oriented and without a pale vertebral stripe; (*g*) lateral surface without a pale midlateral stripe; (*h*) rostral shield with a dark midrostral streak.

Description. The description is based on four specimens collected at the holotype location and includes specimens used in the electrophoresis study.

Measurements. Adult size 36–43 mm SVL; distance from axilla to groin 52.8–55.8% of SVL ($\bar{x}$ = 54.6, n = 4); distance from forelimb to snout 37.2–38.9% of SVL ($\bar{x}$ = 37.9, n = 4); hindlimb length 33.3–37.5% of SVL ($\bar{x}$ = 34.8, n = 4); tail length 136.1% of SVL (n = 1).

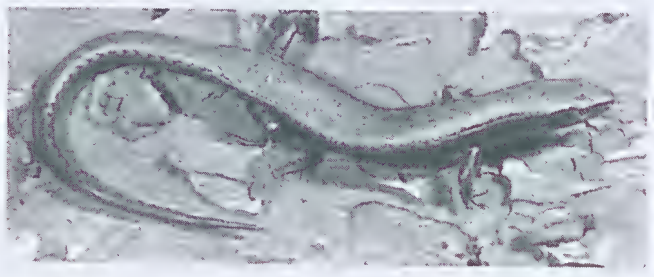

Figure 11. *Caledoniscincus chazeaui* from Koulnoué, Hienghène region.

Scalation. Midbody scales in 28–30 rows ($\bar{x}$ = 29.0, SD = 1.55, n = 4); paravertebral scales in 59–61 rows ($\bar{x}$ = 59.8, SD = 0.96, n = 4); dorsal scales of fourth finger 9 (n = 4); lamellae of fourth finger 12–14 ($\bar{x}$ = 13.4, SD = 0.95, n = 4); dorsal scales of fourth toe 12–13 ($\bar{x}$ = 12.8, SD = 0.5, n = 4); lamellae of fourth toe 21–23 ($\bar{x}$ = 22.3, SD = 0.50, n = 4).

Osteology. Presacral vertebrae 29 (n = 4); postsacral vertebrae 42 (n = 1).

Coloration. The following decryption of colour and pattern is based on two adult females (AMS R138515 and MNHP 1997.3337). Dorsal surface mid brown with a pattern of numerous pale spots, dark-edged at sides, aligned to form a pattern of irregular and merging transverse bars; head with a few fine dark spots anteriorly. Lateral surface between

Figure 12. Isolate limestone outcrops in Hienghène region, typical habitat for *Caledoniscincus chazeaui*.

fore and hindlimbs brown and unmarked, similar to and merging with dorsal surface but becoming lighter approaching venter; between forelimb and ear opening with light and dark markings and either side of eye with bold dark markings; laterodorsal margin between forelimb and ear marked by a narrow, pale, dark-edged stripe, distinct from darker lateral and dorsal colours. Ventral surface pale and unmarked; colour in life unknown.

Details of holotype. Adult female; size 42 mm SVL; distance from axilla to groin 23 mm; distance from forelimb to snout 16 mm; hindlimb length 14 mm; tail length 51 mm, reproduced.

Midbody scales rows 28; paravertebral scale rows 59; dorsal scales of fourth finger 9/9; lamellae of fourth finger 12/12; dorsal scales of fourth toe 12/12; lamellae of fourth toe 22/21.

Presacral vertebrae 29.

Distribution. The type specimens were collected from a single location at Koulnoué on the northeast coast in the vicinity of Hienghène (Fig. 5). Specimens from a disjunct forest patch approximately 10 km south of the type location possibly represent a second location for this species; however, they are only tentatively assigned to *Caledoniscincus chazeaui* pending further field research.

Biology. Restricted to lowland closed forest surrounding limestone outcrops south of Hienghène (Figs. 12, 13). The forest patches are remnants and widely disjunct from one another, the intervening areas being covered with secondary growth or disturbed habitat, either through shifting cultivation, or regular burning to produce extensive areas of grassland.

Additional material examined. A series of 11 specimens (AMS R77823–29, R77832–35) collected 20 years ago from a nearby location (14 km south of the Hienghène River bridge, 20°43'27"S 165°02'00"E) are similar to specimens from the type locality in size, coloration, and habitat preferences. However, these specimens were not part of the electrophoresis study and showed significant differences in a number of scalation characters to the sample from the type locality. For these reasons they were not included in the type series of *Caledoniscincus chazeaui* and are here only tentatively assigned to this species.

Nine specimens from the sample collected 14 km south of the Hienghène River bridge showed the following counts for six variable scalation characters: midbody scales in 30–32 rows ($\bar{x}$ = 30.4, SD = 0.88, n = 9); paravertebral scales in 60–64 rows ($\bar{x}$ = 62.1, SD = 1.36, n = 9); dorsal scales of fourth finger 8–11 ($\bar{x}$ = 8.9, SD = 0.93, n = 9); lamellae of fourth finger 13–16 ($\bar{x}$ = 14.8, SD = 0.90, n = 9); dorsal scales of fourth toe 13–15 ($\bar{x}$ = 13.9, SD = 0.76, n = 9); lamellae of fourth toe 23–32 ($\bar{x}$ = 25.9, SD = 2.69, n = 8). For five of the six scalation characters this sample differs significantly from the type series in having: more midbody scales ($\bar{x}$ = 30.4 *vs* 29, t_{11} = 2.494, P<0.030); more dorsal

Figure 13. Closed forest growing on and around limestone outcrop in Hienghène region.

scales ($\bar{x}$ = 62.1 *vs* 59.8, t_{11} = 3.103, P<0.010); more finger lamellae ($\bar{x}$ = 14.8 *vs* 13.4, t_{11} = 2.655, P<0.022); more toe scales ($\bar{x}$ = 13.9 *vs* 12.8, t_{11} = 2.818, P<0.017); and more toe lamellae ($\bar{x}$ = 25.9 *vs* 22.3, t_{10} = 2.654, P<0.024).

Adult females from the series of specimens collected 14 km south of the Hienghène River bridge during the summer wet season (January) had yolked follicles (1/2, n = 1, SVL 41.5 mm) and oviducal eggs (1/2, n = 1, SVL 42.5 mm), indicating the clutch size of 3 for this population of *Caledoniscincus chazeaui*.

Caledoniscincus cryptos n.sp.

Figs. 5, 14, 15

Type material. HOLOTYPE: AMS R135141 an adult male from 8.3 km from Kouaoua/Canala road intersection on La Foa road, New Caledonia, 21°34'S 165°49'E (R. Sadlier, 18/iii/1990).

Etymology. The species name is from the Greek *cryptos*, for hidden or concealed, and alludes to the recognition of this species through genetic analyses only.

Diagnosis. *Caledoniscincus cryptos* is recognised mainly on the following electrophoretic characteristics: (*i*) it is homozygous (in the only available specimen) for an allele of *Gapdh(A)* which is found nowhere else in our samples; (*ii*) it is also homozygous for *Fbp(C)* and *G3pdh(A)* which are found only as single heterozygotes in non-sympatric *C. orestes* or *C. haplorhinus* respectively; (*iii*) it has fixed differences from morphologically similar *C. renevieri* and *C. auratus* at these three loci; (*iv*) additional fixed differences from *C. renevieri* are found at *Idhp-1* and *Pep:LA*; (*v*) an additional fixed difference from *C. auratus* is seen at *Pgdh*.

Caledoniscincus cryptos can also tentatively be distinguished from most other species of *Caledoniscincus* by the following combination of characters: (*a*) moderately small, 45 mm SVL; (*b*) midbody scales in 30 rows; (*c*) paravertebral scales in 51 rows; (*d*) adult male dorsal colour pattern transversely oriented and without a pale vertebral stripe; (*e*) lateral surface without a pale midlateral stripe; (*f*) rostral shield with a dark midrostral streak.

Description and details of holotype. *Measurements.* Size 45 mm SVL; distance from axilla to groin 24 mm (53.3% of SVL); distance from forelimb to snout 19 mm (42.2% of SVL); hindlimb length 18 mm (40.0% of SVL); tail missing.

Scalation. Midbody scales in 30 rows; paravertebral scales 51; dorsal scales of fourth finger 9/9; lamellae of fourth finger 12/13; dorsal scales of fourth toe 12/13; lamellae of fourth toe 25/25.

Osteology. Presacral vertebrae 29.

Coloration. Dorsal surface mid brown with a pattern of numerous pale spots, dark-edged at the sides, and aligned to form a reticulate pattern of irregular and merging dark transverse bars; head with a few fine dark spots anteriorly. Lateral surface brown and unmarked between fore and hindlimbs, similar to and merging with dorsal surface uppermost and becoming lighter approaching the venter; dark brown to black between forelimb and ear opening, dark markings boldest either side of eye between ear opening and snout; laterodorsal margin between forelimb and ear opening a narrow, pale, stripe distinct from darker lateral and dorsal colours.

Ventral surface pale, unmarked; colour in life unknown.

Distribution. Known only from a single site in the ranges near Col d'Amieu in the central ranges of New Caledonia (Fig. 5).

Biology. Known only from mid altitude closed forest (Fig. 15).

Comparison of species

Electrophoretic results. Fixed differences in sympatry support the recognition of the new taxa described here as distinct species from *Caledoniscincus austrocaledonicus* and *C. haplorhinus* where they occur at the same locality. There are three genetically distinct species found at Koumac (*C. aquilonius, C. auratus* and *C. haplorhinus*). There are a minimum of three fixed differences between any pair of these species at this site, indicating reproductive isolation. There are four fixed differences between *C. terma* and *C. austrocaledonicus* at Mandjélia (the rare IDHP-2 C

allozyme in the latter species not being found there). All three populations of *C. renevieri* occur in sympatry with *C. austrocaledonicus*, there are five fixed and two nearly fixed differences between the taxa at these localities. *Caledoniscincus chazeaui* has ten and *C. cryptos* eight fixed differences from sympatric *C. austrocaledonicus* in the single localities represented in the electrophoretic study.

Otherwise the species of *Caledoniscincus* described here are largely allopatric sibling species restricted to closed forest in the central and northern regions of the island. The genetic data for these species indicate that *C. renevieri* + *C. auratus* + *C. cryptos* form a discrete group. These species are similar in size, adult male coloration, and ventral colour in both sexes (*C. renevieri* + *C. auratus*), and as such may ultimately be recognised as a natural group. Conversely *C. aquilonius* + *C. terma* and *C. chazeaui* are part of a larger group that also includes *C. austrocaledonicus, C. haplorhinus*, and *C. orestes*. No unifying morphological trait that might be indicative of close relationship has been identified in the species in this group.

Figure 14. *Caledoniscincus cryptos* holotype (AMS R135141).

The genetic distance (0.12) separating morphospecies *Caledoniscincus aquilonius* and *C. terma* is relatively small. This is a low value for distances between species in the Scincidae (Kim *et al.*, 1978; Milton *et al.*, 1983; Murphy *et al.*, 1983; Daugherty *et al.*, 1990; Sadlier *et al.*, 1993). *Caledoniscincus aquilonius* and *C. terma* are, however, clearly distinct on a number of morphological characteristics, emphasising that genetic distance alone should not be used as a criterion of species level differentiation.

Morphology. Table 3 shows the range of variation for those mensural, scalation, and coloration characteristics used in the diagnoses in the species accounts, and provides a ready cross-comparison of these key features between all species of *Caledoniscincus*.

Caledoniscincus austrocaledonicus and *Caledoniscincus haplorhinus* are the two most widespread species dealt with here, they are sympatric at a number of locations on New Caledonia, its satellite islands, and the Loyalty Islands. In the south of the main island, Isle des Pins, and Loyalty Islands, *C. austrocaledonicus* lacks a white midlateral stripe, this will readily distinguish it from regionally sympatric *C. haplorhinus*. In the northern and central regions of the main island *C. austrocaledonicus* and *C. haplorhinus* are similar in size, scalation, and certain aspects of coloration, most notably both have a pale midlateral stripe. Samples of either sex in these regions can be distinguished by the expression and positioning of the white midlateral stripe at the ear opening as outlined in the diagnosis of *C. austrocaledonicus*.

The six new species described, *Caledoniscincus aquilonius, C. terma, C. renevieri, C. auratus, C. cryptos*, and *C. chazeaui*, can be distinguished from the other species in the genus as follows:

Caledoniscincus festivus is larger in adult size, has more paravertebral scale rows (similar range for *C. chazeaui*), and more postsacral vertebrae. Adult male *C. festivus* can be further distinguished from adult male *C. aquilonius* by ventral colour (yellow *vs* orange).

Caledoniscincus atropunctatus lacks the dark midrostral streak present in all these species, and has more postsacral vertebrae. *Caledoniscincus atropunctatus* can be further distinguished from adult male *C. aquilonius* by ventral colour (yellow *vs* orange).

Caledoniscincus orestes is larger in adult size, has a pale vertebral stripe in adult males (present also in *C. terma* and some *C. renevieri*), and more postsacral vertebrae. Adult male *C. orestes* can be further distinguished from adult male

Figure 15. Typical closed forest habitat in gully near type locality of *Caledoniscincus cryptos*.

C. terma, C. renevieri, and *C. auratus* by ventral colour (orange *vs* yellow).

Caledoniscincus austrocaledonicus has a pale vertebral stripe in adult males (present also in *C. terma* and some *C. renevieri*). Adult male *C. austrocaledonicus* are further distinguished from adult male *C. terma, C. renevieri*, and *C. auratus* by ventral colour (orange *vs* yellow). *Caledoniscincus austrocaledonicus* (northern and central populations) can also be further distinguished by the presence of a pale midlateral stripe in both sexes.

Caledoniscincus haplorhinus has a pale vertebral stripe in adult males (present also in *C. terma* and some *C. renevieri*), a pale midlateral stripe in both sexes, and more postsacral vertebrae.

Caledoniscincus aquilonius, C. terma, C. renevieri, C. auratus, C. cryptos, and *C. chazeaui* are generally all most similar to one another in scalation, osteology, and to a lesser degree adult male coloration. Significant differences in morphology between these species (except *C. cryptos*) are given below as pairwise comparisons.

Caledoniscincus aquilonius can be distinguished from *C. terma* by: having fewer dorsal scale rows ($\bar{x}$ = 55.8 *vs* 58.9, t_{27} = -3.939, P<0.001), a longer tail ($\bar{x}$ = 154.6 *vs* 135.8% SVL) and more postsacral vertebrae ($\bar{x}$ = 43.5 *vs* 37.5), lacking a pale vertebral stripe (adult *C. terma* have a pale vertebral stripe, most obvious in males), and adult male ventral colour (orange *vs* yellow).

Caledoniscincus aquilonius can be distinguished from *C. renevieri* by: having more midbody scale rows ($\bar{x}$ = 32.2 *vs* 30.3, t_{36} = 6.768, P<0.001), more dorsal scale rows in males ($\bar{x}$ = 55.3 *vs* 52.4, t_{18} = 4.892, P<0.001), more fourth finger lamellae ($\bar{x}$ = 14.4 *vs* 13.6, t_{36} = 3.975, P<0.001), and adult male ventral colour (orange *vs* yellow).

Caledoniscincus aquilonius can be distinguished from *C. auratus* by: having more midbody scale rows($\bar{x}$ = 32.2 *vs* 28.0), more fourth toe lamellae ($\bar{x}$ = 25.2 *vs* 22.9, t_{20} = 4.224, P<0.001), and adult male ventral colour (orange *vs* yellow).

Caledoniscincus aquilonius can be distinguished from *C. chazeaui* by: having more midbody scale rows ($\bar{x}$ = 32.2 *vs* 29.0, t_{17} = 5.191, P<0.001); fewer dorsal scale rows ($\bar{x}$ = 55.8 *vs* 59.8, t_{17} = -5.512, P<0.001); and more fourth toe lamellae ($\bar{x}$ = 25.2 *vs* 22.3, t_{16} = 4.984, P<0.001).

Caledoniscincus terma can be distinguished from *C. renevieri* by: having more midbody scale rows ($\bar{x}$ = 32.3 *vs* 30.4, t_{22} = 4.106, P<0.001), more dorsal scale rows in both males ($\bar{x}$ = 57.3 *vs* 52.4, t_{14} = 6.183, P<0.001) and females ($\bar{x}$ = 59.6 *vs* 54.9, t_{19} = 4.744, P<0.001), a shorter tail ($\bar{x}$ = 136.3 *vs* 140.2% SVL) with fewer postsacral vertebrae ($\bar{x}$ = 37.5 *vs* 42.7), and to a lesser extent in adult male dorsal coloration (pale vertebral stripe present *vs* usually absent in *C. renevieri*).

Caledoniscincus terma can be distinguished from *C. auratus* by: having more midbody scale rows ($\bar{x}$ = 32.4 *vs* 28.0), more dorsal scale rows ($\bar{x}$ = 58.9 *vs* 53.6, t_{20} = 5.555, P<0.001), more fourth toe lamellae ($\bar{x}$ = 25.4 *vs* 22.9, t_{20} = 4.841, P<0.001), a shorter tail ($\bar{x}$ = 136.3 *vs* 146.8% SVL) with fewer postsacral vertebrae ($\bar{x}$ = 37.5 *vs* 44.0), and adult male dorsal coloration (pale vertebral stripe present *vs* absent in *C. auratus*).

Caledoniscincus terma can be distinguished from *C. chazeaui* by: having more midbody scale rows ($\bar{x}$ = 32.4 *vs* 29.0, t_{16} = 6.601, P<0.001), more fourth toe lamellae ($\bar{x}$ = 25.4 *vs* 22.3, t_{16} = 5.974, P<0.001), fewer postsacral vertebrae ($\bar{x}$ = 37.5 *vs* 42.0), and adult male dorsal coloration (pale vertebral stripe present *vs* absent in *C. chazeaui*).

Caledoniscincus renevieri can be distinguished from *C. auratus* by: having more midbody scale rows (30–32 *vs* 28), otherwise in scalation and adult male colour *C. renevieri* is most similar to *C. auratus* from Koumac.

Caledoniscincus renevieri can be distinguished from the type series of *C. chazeaui* by: having fewer dorsal scale rows ($\bar{x}$ = 53.6 *vs* 59.8, t_{25} = -5.902, P<0.001).

Caledoniscincus auratus can be distinguished from *C. chazeaui* by: having fewer dorsal scale rows ($\bar{x}$ = 53.6 *vs* 59.8, t_{10} = -9.703, P<0.001).

Caledoniscincus cryptos can be distinguished from adult male *C. aquilonius* by lacking a broad pale laterodorsal margin and from *C. terma* by lacking a pale vertebral stripe. *Caledoniscincus cryptos* is most similar in overall appearance to *C. renevieri* and *C. auratus* in having a reticulate patterned dorsal surface (except some *C. renevieri* which have pale vertebral markings). Although no meaningful comparison of scalation can be made between *C. cryptos* and either *C. renevieri* or *C. auratus*, the values for *C. cryptos* generally fall within a single standard deviation from the mean for all scalation characters of both species.

Discussion

The results presented here have doubled the known number of species in the genus *Caledoniscincus* to 11. Relationships between the three isolated populations of *C. orestes* have yet to be investigated and may yield further cryptic species in the complex. Such a significant increase in diversity in the genus was unexpected on the basis of existing collections prior to 1990. Only a few of the taxa described here were represented in museum collections prior this date, and then generally only as a small number of "anomalous" specimens in particular collections. The increase in species diversity has resulted from extensive field research over the past eight years that has targeted these "anomalous" specimens and the opportunity to collect in areas not previously investigated.

The results in this paper have several biogeographical implications. The distinction between northern and southern herpetofaunas previously identified (Bauer & Sadlier, 1993) has predominantly been based on specific and generic endemism in the extensive ultramafic block that covers much of the southern third of the island. *Caledoniscincus* now shows extensive speciation north of the southern ultramafic block involving a complex of largely allopatric endemics. The presence of sister species of *Tropidoscincus* in the north (*T. variabilis*) and south (as defined by the extensive southern ultramafic block—*T. rohssii*) also reflect the distinction between northern and southern herpetofaunas, and is similar in distribution to the variation in coloration seen in the widespread species *C. austrocaledonicus*. The northeastern ranges have also been

identified as a significant area of endemism for lizards (Bauer & Sadlier, 1993). The description of *C. terma* from Mt Mandjélia increases the number of species endemic to this region to four (the scincid lizards *C. terma* and an undescribed *Nannoscincus*, and the gekkonid lizards *Bavayia ornata* and *Bavayia validiclavis*). The results of our research indicate that the distribution patterns of the forest-restricted species described in this paper may reflect finer scale biogeographic regions across the central and northern regions of the island than previous studies have indicated. Further studies on widespread lizard taxa are required to see if similar distribution patterns occur.

Despite extensive field research by the authors in New Caledonia over the past eight years most of the new taxa described here are still only known from a few locations. Further field research is required to delimit accurately the distributions of these species.

Conservation status

The conservation status of the species described in this paper are assessed below and follows Bauer & Sadlier (1993) in utilising a combination of known sites to assess distribution, average number of records per site as an indication of relative abundance, and known threats to assess vulnerability. The species are then categorised as per the current IUCN (1996) criteria where appropriate.

Caledoniscincus austrocaledonicus and *C. haplorhinus* are widespread and common species, neither are considered threatened and are not discussed further.

Of the six closed forest dependent species described here *Caledoniscincus aquilonius* and *C. renevieri* are the least restricted in distribution. *Caledoniscincus aquilonius* is likely to be the most widespread of the six species described here. Aside from the type location at Mt Panié it is known from four scattered localities in the far northeast ranges from near sea level to 670 m altitude, and in this region is likely to occur where suitable closed forest habitat is present. Populations of *C. aquilonius* in this region are relatively secure although lowland populations are likely to be threatened by loss of habitat as a result of clearing for agriculture and the impact of fire on forest margins. Extralimital populations of *Caledoniscincus aquilonius* are known from Koumac Caves on the west coast and the ranges west of Poindimié. The conservation status of these extralimital populations is difficult to assess until more data on the species distribution are available, particularly in the south and far north of the species range. The population of *C. aquilonius* from Koumac Caves is considered the most vulnerable. It is known only from the seasonally dry closed forests at Koumac Caves where remnant closed forest at the edge of the limestone outcrops is threatened by clearing for agriculture, degradation to the forest understorey and litter layer by stray cattle from adjacent farms, and fire. Because of its isolated nature and the threats posed by human activities the Koumac population of *C. aquilonius* could be regarded as potentially endangered. Research to determine the distinctiveness of this population is required before its conservation significance can be assessed under the current IUCN (1996) classification system.

Caledoniscincus renevieri is known from three sites in general proximity to one another in the central ranges from low to mid altitude, and in this region is likely to occur where there is suitable closed forest habitat. Populations of *C. renevieri* in this region are relatively secure although, like *C. aquilonius*, lowland populations are likely to be threatened by loss of habitat due to clearing for agriculture and fire burning the forest margins. The impact of such activities is most clearly seen at Adio Caves where closed forest habitat has been cleared to the edge of the outcropping limestone.

It is likely that with further field research both *C. aquilonius* and *C. renevieri* will become known from more localities, and both species will prove to be both moderately widespread and secure within the discrete regions in which they occur.

Two species, *Caledoniscincus auratus* and *C. chazeaui* are very restricted in distribution. Both are known to be, or have been, generally common where they occur, but are likely to be adversely affected by habitat disturbance.

Caledoniscincus auratus is known with certainty only from the seasonally dry closed forests at Koumac Caves. At this locality, closed forest at the edge of the limestone outcrops is threatened by clearing for agriculture, degradation to the forest understorey and litter layer by stray cattle from adjacent farms, and fire. Situated on the lowlands of the west coast, this forest is seasonally dry and is likely to be particularly vulnerable to the impact of fires which could alter the canopy and modify the structural and microclimate characteristics, in turn possibly adversely affecting the population of *C. auratus*. Recently a sample of three specimens containing two adult males similar in coloration to adult males from the type series of *C. auratus* was collected from near Kaala-Gomen, approximately 20 km south of Koumac. These specimens also were from closed forest habitat in the vicinity of limestone outcrops, and it is possible they represent the occurrence of a second population of this species in the region. Because of its apparently restricted distribution i.e. known with certainty from only a single isolated location, but possibly present at a second nearby location, *C. auratus* should at the very least be regarded as Vulnerable:D2 under the current IUCN (1996) classification system (area of occupancy <100 km^2 or number of locations <5). When the threats posed by human activities at the type locality are also taken into account *C. auratus* could potentially be assessed as Endangered:B1/2c (extent of occurrence <100 km^2; known to exist at one, possibly two, locations; continuing decline in area, extent and/or quality of habitat). However, the extent of the species distribution in the region needs to be determined, and the extent of decline in both area and quality of habitat to known sites needs to established.

Caledoniscincus chazeaui is similarly restricted in distribution and habitat preference. It is known with certainty only from remnant closed forest at the edge of near-coastal limestone outcrops at Koulnoué, south of Hienghène in the northeast of the island. It was collected in 1992 in an area of closed forest habitat adjacent to limestone outcrops that bordered local gardens. Since that time the area has been revisited on two occasions (1994 and 1995)

and *C. chazeaui* was not observed either time. These years were atypically dry and it is possible the local distribution of *C. chazeaui* may fluctuate with seasonal change, to be restricted to more mesic sites under suboptimal conditions. Whatever the reason for its apparent absence from this site during these latter visits, it suggests this species might be sensitive to climatic or human alteration to the habitat. Other areas of closed forest surrounding other outcrops in the region south of Hienghène are similarly developed. Samples from a nearby site tentatively assigned to this species were collected in 1978. This site was visited again in 1992 and appeared to have changed markedly in the intervening 13 years from being uninhabited to now settled with intensive subsistence agriculture carried out to the margin of the closed forest at the base of the limestone outcrops. Because of the isolated nature of the known populations and the threats posed by human activities, *C. chazeaui* could be regarded as Endangered:B1/2c under the current IUCN (1996) classification system (extent of occurrence <100 km^2; one, possibly two, isolated subpopulations with a reduced probability of recolonization, if once extinct; continuing decline in area, extent and/or quality of habitat).

Caledoniscincus terma is very restricted in distribution but common where it occurs. It is not considered under any immediate threat, but because of its restricted distribution the population could be regarded as Vulnerable:D2 under the current IUCN (1996) classification system (area of occupancy <100 km^2 or number of locations <5).

Caledoniscincus cryptos is known only from a single specimen. Field research in the general area where *C. cryptos* was collected is likely to show it to be more widespread in distribution, though its apparent rarity and absence from other sites collected in the vicinity of Col d'Amieu is perplexing. For these reasons it regarded as Data Deficient under the current IUCN (1996) classification system.

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Table 1. Allozymic frequencies in *Caledoniscincus* populations. The enzyme name, abbreviation and E.C. number are given in the first row of data for each locus. Numbers in the next row indicate sample sizes. Population listings loosely follow a North to South and West to East order. *Caledoniscincus aquilonius* 1 is from Koumac, *C. aquilonius* 2 from Mt Panié and *C. aquilonius* 3 from Kavaatch. *Caledoniscincus renevieri* 1 is from Mt Aoupinié, *C. renevieri* 2 from Adio Caves and *C. renevieri* 3 from Col des Roussettes. Species' names abbreviated to first five letters.

locus	*aquil.* 1	*aquil.* 2	*aquil.* 3	*terma.*	*aurat.*	*renev.* 1	*renev.* 2	*renev.* 3	*crypt.*	*chaze.*	*orest.*	*haplo.*	*austr.*
AAT1	***aspartate aminotransferase* 2.6.1.1**												
(n)	8	6	5	7	2	3	4	6	1	4	5	23	77
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–	1.000	1.000	–
B	–	–	–	–	–	–	–	–	–	–	–	–	1.000
C	–	–	–	–	–	–	–	–	–	1.000	–	–	–
AAT2	***aspartate aminotransferase* 2.6.1.1**												
(n)	8	6	6	7	2	3	4	6	1	4	5	23	79
A	–	–	–	–	–	–	–	–	–	–	–	–	
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
FBP	***fructose bisphosphatase* 3.1.3.11**												
(n)	7	6	6	6	2	2	3	5	1	4	5	23	78
A	0.071	–	0.083	–	0.250	–	–	–	–	–	–	0.087	0.019
B	0.929	1.000	0.917	1.000	0.750	1.000	1.000	1.000	–	1.000	–	0.913	0.981
C	–	–	–	–	–	–	–	–	1.000	–	0.100	–	
D	–	–	–	–	–	–	–	–	–	–	0.900	–	
FH1	***fumarate hydratase* 4.2.1.2**												
(n)	7	6	6	5	2	3	2	5	1	4	5	22	72
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.951
B	–	–	–	–	–	–	–	–	–	–	–	–	0.049
FH2	***fumarate hydratase* 4.2.1.2**												
(n)	8	6	6	7	9	3	4	6	1	4	5	22	73
A	–	–	–	–	0.056	–	–	–	–	–	–	–	0.014
B	–	–	–	–	0.944	1.000	1.000	1.000	1.000	–	–	–	0.288
C	1.000	1.000	1.000	1.000	–	–	–	–	–	1.000	–	1.000	0.699
D	–	–	–	–	–	–	–	–	–	–	1.000	–	–
GAPDH	***glyceraldehyde-3-phosphate dehydrogenase* 1.2.1.12**												
(n)	8	6	6	7	9	3	3	6	1	4	5	23	74
A	–	–	–	–	–	–	–	–	1.000	–	–	–	–
B	–	–	–	–	–	–	–	–	–	–	–	–	0.061
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–	1.000	1.000	1.000	0.770
D	–	–	–	–	–	–	–	–	–	–	–	–	0.169
G3PDH	***glycerol-3-phosphate dehydrogenase* 1.1.1.8**												
(n)	4	1	2	5	1	3	4	5	1	2	3	21	62
A	–	–	–	–	–	–	–	–	1.000	–	–	–	0.008
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–	1.000	1.000	–	0.992
C	–	–	–	–	–	–	–	–	–	–	–	1.000	–
GPI	***glucosephosphate isomerase* 5.3.1.9**												
(n)	8	6	6	7	9	3	3	6	1	4	5	21	77
A	0.625	1.000	0.167	1.000	0.889	1.000	1.000	1.000	0.500	1.000	1.000	1.000	1.000
B	–	–	–	–	0.111	–	–	–	0.500	–	–	–	–
C	0.375	–	0.833	–	–	–	–	–	–	–	–	–	–
IDHP-1	***isocitrate dehydrogenase* (NADP$^+$) 1.1.1.42**												
(n)	8	6	6	7	9	3	4	6	1	4	5	23	78
A	–	–	–	–	–	–	–	–	–	–	–	1.000	–
B	–	–	–	–	–	1.000	1.000	1.000	–	–	–	–	–
C	–	–	–	–	–	–	–	–	–	–	1.000	–	1.000
D	–	–	–	–	1.000	–	–	–	1.000	–	–	–	–
E	–	–	–	–	–	–	–	–	–	–	–	–	–
null	1.000	1.000	1.000	1.000	–	–	–	–	–	1.000	–	–	–
IDHP-2	***isocitrate dehydrogenase* (NADP$^+$) 1.1.1.42**												
(n)	8	6	6	7	9	3	4	6	1	4	5	23	78
A	–	–	–	–	–	–	–	–	–	–	–	1.000	–
B	1.000	1.000	0.917	–	0.111	1.000	1.000	1.000	1.000	1.000	–	–	–
C	–	–	–	0.357	–	–	–	–	–	–	–	–	–
D	–	–	0.083	–	0.889	–	–	–	–	–	–	–	0.994
E	–	–	–	0.643	–	–	–	–	–	–	–	–	0.006
F	–	–	–	–	–	–	–	–	–	–	1.000	–	–

Table 1. Continued ...

locus	*aquil.* 1	*aquil.* 2	*aquil.* 3	*terma.*	*aurat.*	*renev.* 1	*renev.* 2	*renev.* 3	*crypt.*	*chaze.*	*orest.*	*haplo.*	*austr.*
LDH-1	**L-*lactate dehydrogenase* 1.1.1.27**												
(n)	8	5	6	7	8	3	4	6	1	4	1	23	79
A	1.000	1.000	1.000	1.000	0.750	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	–	–	–	–	0.250	–	–	–	–	–	–	–	–
LDH-2	**L-*lactate dehydrogenase* 1.1.1.27**												
(n)	8	5	6	7	9	3	4	6	1	4	5	22	77
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH-1	***malate dehydrogenase* 1.1.1.37**												
(n)	8	6	6	4	9	3	4	6	1	4	5	23	77
A	–	–	–	–	1.000	1.000	1.000	1.000	1.000	1.000	–	–	–
B	1.000	1.000	1.000	1.000	–	–	–	–	–	–	1.000	1.000	1.000
MDH-2	***malate dehydrogenase* 1.1.1.37**												
(n)	8	6	6	7	9	3	4	6	1	4	5	23	79
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI	***mannose-6-phosphate isomerase* 5.3.1.8**												
(n)	8	6	6	7	2	3	3	6	1	4	5	22	78
A	–	–	–	0.071	–	–	–	–	–	–	–	0.409	0.019
B	1.000	1.000	1.000	0.929	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.591	0.974
C	–	–	–	–	–	–	–	–	–	–	–	0.006	–
PEP:LA	***peptidase* leucine-alanine substrate 3.4.13.-**												
(n)	6	6	6	2	2	2	2	3	1	4	5	16	64
A	–	–	–	–	–	–	–	–	–	–	–	–	0.016
B	–	–	–	–	–	0.500	1.000	–	–	1.000	–	0.250	0.070
C	1.000	1.000	1.000	1.000	–	0.500	–	1.000	–	–	1.000	0.750	0.914
D	–	–	–	–	1.000	–	–	–	1.000	–	–	–	–
PEP:LGG	***peptidase* leucine-glycine-glycine substrate 3.4.13.-**												
(n)	7	6	6	7	2	3	4	6	1	4	1	22	75
A	–	–	0.083	–	1.000	–	–	–	–	1.000	–	0.045	0.033
B	0.929	0.750	0.750	0.857	–	1.000	1.000	0.167	–	–	1.000	0.955	0.933
C	0.071	0.250	0.167	0.143	–	–	–	0.833	0.500	–	–	–	0.033
D	–	–	–	–	–	–	–	–	0.500	–	–	–	–
PEP:PP	***peptidase* phenylalanine-proline substrate 3.4.13.-**												
(n)	8	5	6	7	2	3	4	6	1	4	5	23	76
A	–	–	0.167	0.214	1.000	1.000	1.000	1.000	1.000	–	1.000	0.022	0.039
B	1.000	1.000	0.833	0.786	–	–	–	–	–	1.000	–	0.978	0.961
PGDH	***phosphogluconate dehydrogenase* 1.1.1.44**												
(n)	8	5	6	7	9	3	4	6	1	4	5	23	77
A	–	–	–	–	–	–	–	–	–	–	–	–	0.006
B	–	–	–	–	–	–	–	–	–	–	–	–	0.013
C	–	–	–	–	–	–	–	–	–	–	–	–	0.006
D	–	–	–	–	–	1.000	1.000	1.000	1.000	–	–	0.065	0.065
E	–	–	–	1.000	1.000	–	–	–	–	1.000	–	–	–
F	1.000	1.000	0.917	–	–	–	–	–	–	–	0.800	0.891	0.909
G	–	–	0.083	–	–	–	–	–	–	–	0.200	–	–
H	–	–	–	–	–	–	–	–	–	–	–	0.043	–
PGM	***phosphoglucomutase* 5.4.2.2**												
(n)	8	6	6	7	9	3	4	6	1	4	5	23	79
A	–	–	–	–	–	–	0.250	–	–	–	–	–	–
B	1.000	1.000	1.000	0.929	1.000	1.000	0.750	1.000	1.000	1.000	–	–	–
C	–	–	–	0.071	–	–	–	–	–	–	1.000	0.957	0.222
D	–	–	–	–	–	–	–	–	–	–	–	0.043	0.778

Table 2. Matrix of genetic distances between *Caledoniscincus* populations. The figures below the diagonal are Nei (1978) unbiased genetic distances and those above the diagonal are the percentage of fixed differences. Population identifications are the same as for Table 1. *Idhp-1* nulls are not included in fixed difference calculations; *austro.* = *austrocaledonicus*.

population:	1	2	3	4	5	6	7	8	9	10	11	12	13
1 *C. aquilonius* 1		0	0	15	30	20	25	20	40	20	30	20	15
2 *C. aquilonius* 2	0.007		0	15	30	20	25	20	40	20	30	20	15
3 *C. aquilonius* 3	0.010	0.035		15	20	15	20	15	35	15	25	20	10
4 *C. terma*	0.106	0.097	0.128		25	20	25	20	40	20	25	25	15
5 *C. auratus*	0.529	0.506	0.518	0.400		20	20	20	25	25	40	35	25
6 *C. renevieri* 1	0.321	0.312	0.342	0.345	0.271		0	0	25	35	30	30	15
7 *C. renevieri* 2	0.382	0.372	0.406	0.407	0.295	0.010		5	30	35	35	30	15
8 *C. renevieri* 3	0.346	0.315	0.350	0.361	0.281	0.044	0.092		20	35	30	30	15
9 *C. cryptos*	0.715	0.695	0.705	0.777	0.345	0.350	0.375	0.329		45	45	50	30
10 *C. chazeaui*	0.298	0.277	0.322	0.275	0.356	0.376	0.364	0.423	0.719		45	30	20
11 *C. orestes*	0.370	0.365	0.389	0.375	0.580	0.439	0.486	0.475	0.804	0.784		25	20
12 *C. austro.*	0.258	0.250	0.300	0.289	0.723	0.539	0.568	0.599	0.961	0.580	0.380		20
13 *C. haplorhinus*	0.246	0.237	0.281	0.285	0.577	0.488	0.531	0.526	0.997	0.509	0.327	0.305	

Table 3. Distribution of key diagnostic characters for all species of *Caledoniscincus*; *austr.* s = southern population (Noumea), *austr.* n = northern and central populations (Mt Aoupinié), species' names abbreviated to first five letters.

	SIZE (SVL) range	TL (% SVL) range	TL (% SVL) $\bar{x}$	DSR range	DSR $\bar{x}$	MBR range	MBR $\bar{x}$	post-sacral range	post-sacral $\bar{x}$	vertebral stripe	mid-lateral stripe	dark midrostral streak	adult male ventral colour
aquil.	39–49	146–163	155	54–58	55.8	30–34	32.2	40–44	43.5	yes	yes	no	orange
terma.	41–50	131–140	136	55–63	58.9	32–34	32.4	37–38	37.5	no	yes	no	yellow
renev.	37–51	127–154	140	51–58	53.6	30–32	30.3	41–44	42.7	+/–	yes	no	yellow
aurat.	38–51	141–151	147	52–55	53.6	28	–	43–45	44.0	yes	yes	no	yellow
chaze.	36–43		136	59–61	59.8	28–30	29.0		42	yes	yes	no	?
crypt.	45	–	–		51		30	–	–	yes	yes	no	?
orest.	47–63	–	–	55–63	57.9	32–36	32.8		50	no	yes	no	orange
austr. s	39–46	–	155	56–62	59.9	28–30	29.5	–	>46	no	yes	no	orange
austr. n	44–57	–	≈150	58–65	61.2	30–32	31.2	–	>50	no	no	no	orange
haplo.	42–55	156–174	165	59–67	63.0	28–32	30.0	51–55	52.3	no	no	no	yellow
festi.	59–72	131–160	150	60–66	61.9	32–34	32.9	49–56	52.1	yes	yes	no	yellow
atrop.	38–53	142–153	150	51–60	55.9	28–32	29.6	49–51	50	yes	yes	yes	?yellow

Appendix 1

Registration numbers and corresponding tissue numbers (in brackets) for the specimens of *Caledoniscincus* used in the electrophoretic study. For each species a generalised place name for each population sampled is given, and listed in a north to south order.

Caledoniscincus atropunctatus

Col d'Amieu	R144282 (2342), R144383 (2303), R144174 (2541), R144175 (2542)
Koumac	R144295 (2596)

Caledoniscincus festivus

Mt Koghis	R135125 (0176)
Col d'Amieu	R144182 (2488)

Caledoniscincus orestes

Mt Panié	R144217 (2304), R144221 (2482), R144222 (2483), R144223 (2484), R144224 (2485)

Caledoniscincus austrocaledonicus

Mandjélia	R146322 (2830), R146323 (2831), R146324 (2832), R146325 (2833)
Ouaïème	R144239 (2293), R144240 (2294), R144243 (2550), R144244 (2551), R144245 (2552), R144246 (2553)
Koulnoué	R138326 (0817), R138327 (0818)
Poindimié	R144270 (2563), R144271 (2564), R144265 (2588), R144266 (2589), R144267 (2590), R144268 (2591)
Mt Aoupinié	R146386 (2887), CAS 198720 (2888), CAS 198725 (2885), CAS 198726 (2886), R146379 (3001), R146380 (3002)
Adio Caves	R146503 (3030), R146504 (3031)
Poya	CAS 198672 (2820), R146307 (3070), R146308 (3071), R146309 (3072)
Col des Roussettes	R146398 (2906), R146432 (2944)
Col d'Amieu	R144163 (2308), R144164 (2309), R144165 (2310), R144166 (2543), R144167 (2544), R144168 (2545)
Sarraméa	R144112 (2315), R144113 (2316), R144114 (2546), R144115 (2547), R144116 (2548), R144117 (2549)
Plateau de Dogny	R144137 (2284), R144138 (2285), R144284 (2489), R144285 (2490), R144286 (2491), R144287 (2492)
Mt Do	CAS 198674 (2922)
Tomo	R146294 (2810), R146295 (2811), R146296 (2812), R146297 (2813)
Nouméa	R135114 (0165), R135115 (0166), R135116 (0167), R135117 (0168), R135118 (0169)
Mt Koghis	R135126 (0177), R135127 (0178)
Rivière Bleue	R135133 (0182), R135134 (0183), R135135 (0184), R135136 (0185)
Ile des Pins	R138559 (0804), R138560 (0805), R138561 (0845), R138646 (0846)

Caledoniscincus haplorhinus

Koumac	R144284 (2289), R144285 (2290), R144257 (2538), R144258 (2539), R144288 (2593), R144289 (2594)
Tomo	R146301 (2816), R146302 (2817), CAS 198669 (2818), CAS 198670 (2819)
Plage de Pindaï	R146461 (2993), R146462 (2994), R146463 (2995), R146464 (2996)
Plage de Ouano	R146436 (2946), CAS 198763 (2947), R146437 (2948), CAS 198764 (2594)
Nouméa	R135119 (0170), R135120 (0171), R135121 (0172), R135122 (0173), R135123 (0174)

Caledoniscincus aquilonius

Kavaatch	R144249 (2555), R144252 (2296), R144250 (2556), R144251 (2557), R144253 (2297), CAS 182062 (0830)
Mt Panié	R144199 (2322), 144206 (2529), R144227 (2480), R144200 (2323), R144207 (2530), R144228 (2481)
Koumac	R144296 (2298), R144297 (2299), R144259 (2540), R144380 (2597), R146338 (2839), R146339 (2840), R146340 (2841), R146341 (2842)

Caledoniscincus terma

Mt Mandjélia	R146316 (2827), CAS 198680 (2828), R146346 (2844), R146344 (3003), R146345 (3004), R146320 (3005), R146321 (3006)

Caledoniscincus renevieri

Mt Aoupinié	R146382 (2932), R146383 (2933), R146384 (2934)
Adio Caves	R146499 (3026), R146500 (3027), R146501 (3028), AMB 4466 (3029)
Col des Roussettes	R146392 (2895), R146393 (2896), R146394 (2897), R146395 (2898), CAS 198745 (2938), R146423 (3008)

Caledoniscincus chazeaui

Koulnoué	CAS 182073 (0819), CAS 182074 (0820), R138515 (0821), R138516 (0822)

Caledoniscincus auratus

Koumac	R144298 (2300), R144299 (2301), R144300 (2302), R144301 (2476), R144302 (2477), R144303 (2478), R144304 (2479), R144381 (2598), R144382 (2599)

Caledoniscincus cryptos

Col d'Amieu	R135141 (0188)

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The Scincid Lizard Genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: Description of a New Species and Review of the Biology, Distribution and Morphology of *Sigaloseps deplanchei* (Bavay)

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ABSTRACT. *Sigaloseps* is a genus of two species of scincid lizards endemic to the southern ultramafic region of New Caledonia in the southwest Pacific. The morphology, distribution, and habits of the moderately widespread species *Sigaloseps deplanchei* are reviewed. The other species in the genus represents a new taxon known only from two high altitude sites above 1,000 m asl. The conservation status of both species is assessed. *Sigaloseps deplanchei* is not regarded as threatened. The new species, *Sigaloseps ruficauda*, by virtue of its restricted distribution and habitat preference, is likely to be adversely affected by habitat modification, and is regarded as vulnerable.

SADLIER, ROSS A., & AARON M. BAUER, 1999. The scincid lizard genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: description of a new species and review of the biology, distribution and morphology of *Sigaloseps deplanchei* (Bavay). *Records of the Australian Museum* 51(1): 83–91.

The generic name *Sigaloseps* was originally proposed by Sadlier (1986) to include the small New Caledonian scincid lizard *Lygosoma deplanchei* Bavay (1869). At that time it was regarded as a monotypic genus and known only from a few specimens from a few localities in the south of New Caledonia.

Field research in the intervening decade has greatly increased both the amount of material available and our knowledge of the distribution and habits of *Sigaloseps deplanchei*. These data indicate that *S. deplanchei* is endemic to moist, closed forest in the ultramafic block in the southern third of the island. It is relatively common in this habitat type and not considered to be under any immediate threat. Investigation of high altitude habitats in 1995 resulted in the discovery of a second species of *Sigaloseps* in southern New Caledonia. This species is so far known only from two sites in geographical proximity to one another, Mt Mou and Mt Ouin. The new *Sigaloseps* is one of only two species of skink known to be restricted to high altitude habitat in southern New Caledonia (the other being an undescribed species of *Marmorosphax*) and is likely to occur only as scattered relictual populations in

suitably moist habitats around 1,000 m in altitude. Because of its apparently restricted distribution and habitat preferences this new species of *Sigaloseps* is considered vulnerable.

In this paper we provide an overview of the biology and morphology of *Sigaloseps deplanchei* and describe the new species.

Materials and methods

Acronyms. Specimen abbreviations are prefixed as follows: Australian Museum (AMS); California Academy of Sciences (CAS); Museum National d'Histoire Naturelle Paris (MNHN), Naturhistorisches Museum, Basel (NHMB); Auckland Museum (AIM).

Measurements. The following measurements were made for each adult specimen, as determined by reproductive maturity and/or obvious size classes, where possible: snout to vent length—measured from tip of snout to caudal edge of anal scales; axilla to groin distance—measured from middle of base of forelimb to middle of base of hindlimb; forelimb to snout length—measured from tip of snout to middle of base of forelimb; hindlimb length—measured from middle of base of hindlimb to tip of fourth toe including nail; tail length—measured from caudal edge of anal scales to tip of tail, on complete original tails only. Body measurements are expressed as percentages of snout to vent length (SVL) in the taxon accounts.

Scalation. Head scalation terminology generally follows Taylor (1935) as described and figured by Sadlier (1986), abbreviations in brackets are those used in Table 1; midbody scale rows (MBR)—number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scales (DSR)—number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at level of vent opening; fourth finger (FFS) and toe (FTS) scales—number of dorsal scales on fourth digit of hand and foot, distal scale contains claw, basal scale of fourth finger incorporates basal scale of adjacent third finger, and basal scale of fourth toe broadly contacts basal scale of adjacent third toe; fourth finger (FFL) and toe (FTL) lamellae—number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at, or proximal to, a point level with intersection of third and fourth digits. Bilateral scalation characters were scored on both sides and the mean value used in the species accounts and tables, but are expressed individually for types as left/right values respectively. Sexual dimorphism in paravertebral scales (the scalation character most likely to exhibit this trait) was assessed using independent two-sample *t*-test for the largest population. Variation between populations in scalation was assessed using independent two-sample *t*-tests for all scalation characters. Characters with a P value ≤0.05 are provided, however only those with a high P value ≤0.001 are considered likely to reflect unambiguous differences between populations.

Osteology. Specimens were *X*-rayed for counting the number of presacral vertebrae and postsacral vertebrae on complete original tails only.

Reproduction. The distribution of eggs in gravid females is expressed as left/right values for the number of eggs in the left and right oviducts respectively.

Species descriptions

Genus *Sigaloseps* Sadlier, 1986.

This genus contains two species of small to moderately small scincid lizard, *Sigaloseps deplanchei* and *Sigaloseps ruficauda* n.sp., both endemic to New Caledonia. Both species are restricted to the south of the island, *S. deplanchei* is moderately widespread in closed forest habitat throughout its range and *S. ruficauda* is known only from two high altitude sites.

Type species. *Lygosoma deplanchei* Bavay, 1869: 23.

Diagnosis. *Sigaloseps* is identified as a member of the *Eugongylus* group of skinks (Greer, 1979) by possessing the following combination of synapomorphies: parietal scales meet behind the interparietal; parietal bordered along its posterior edge by upper secondary temporal/s and transversely enlarged nuchal scale; presacral vertebrae >26.

Within the *Eugongylus* group, *Sigaloseps* possesses the following suite of derived character states: (*a*) supranasals absent; (*b*) frontoparietals fused; (*c*) ear lobules very small; (*d*) body scales smooth; (*e*) basal finger scales of 3rd and 4th fingers generally fused to form a single broad scale. It also has the atlantal arches fused to the intercentrum and is therefore included in the monophyletic *Pseudemoia* subgroup (Greer, 1989).

Sigaloseps ruficauda n.sp.

Figs. 1–6

Type material. HOLOTYPE: AMS R146482 Mt Mou, New Caledonia 22°03'45"S 166°20'39"E (R. Sadlier and P. Rowland, 16.i.95). PARATYPES: MNHN 1997.3325 (formerly AMS R146481) Mt Mou, New Caledonia 22°04'01"S 166°20'34"E; AMS R146483, R146196–97, MNHN 1997.3326 (formerly AMS R146198) same data as holotype; AMS R148004 Mt Mou, New Caledonia 22°03'42"S 166°20'41"E; AMS R148024 Mt Ouin 22°00'34"S 166°27'26"E.

Etymology. The species epithet is from the Latin *rufus*, for red, and *cauda*, for tail. The name alludes to the bright reddish colour of the tail in both sexes of this species.

Diagnosis. *Sigaloseps ruficauda* is distinguished from *Sigaloseps deplanchei* by the following combination of characters: (*a*) larger adult size (maximum SVL 60 *vs* 46 mm); (*b*) more numerous paravertebral scales (53–60 *vs* 46–56); (*c*) longer tail (tail length 150 *vs* 100% SVL); (*d*) more postsacral vertebrae 47–49 *vs* 35–39; (*e*) a uniform bright orange to reddish tail colour overall in both sexes (*vs* dull orange markings); (*f*) and well defined and

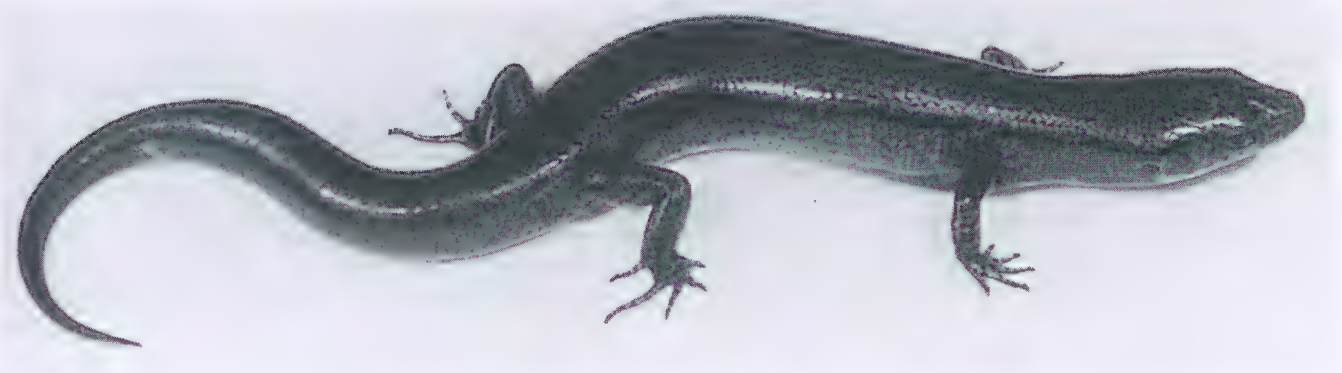

Figure 1. Paratype of *Sigaloseps ruficauda* n.sp. (AMS R146483), an adult female.

continuous dorsolateral markings between eye and forelimb (*vs* a series of broken markings in this region).

Description. The species is known from five adults 38–60 mm SVL, and three juveniles 25–27 mm SVL. Measurements are for adults only.

Measurements. Distance from axilla to groin 54.7–58.3% SVL ($\bar{x}$ = 55.7, n = 5); distance from forelimb to snout 35.7–39.6% SVL ($\bar{x}$ = 37.8, n = 5); hindlimb length 30.0–36.8% SVL ($\bar{x}$ = 32.9, n = 5); tail length 152.6% SVL (n = 1).

Scalation. Frontonasal broader than long; prefrontals narrowly-moderately separated; frontal longer than wide; frontoparietals fused; interparietal distinct; parietal bordered by a nuchal and upper secondary temporal scale; primary temporal single; upper secondary temporal single and overlapping lower; lower secondary temporal single; tertiary temporals two; postlabials two; nasals moderately large, moderately to widely separated; supraciliaries usually seven (83.3%), rarely six or eight; upper labials seven, fifth subocular and contacting lower eyelid; lower labials six, first two contacting postmental; large chinshields three, members of first pair in broad contact, members of second pair separated by one scale, members of third pair separated by three scales, all chin scales flush with lower labials.

Lower eyelid with a centrally located semi-transparent disc, length approximately 30% of total eye length.

Ear opening moderately large, with small acute lobules anteriorly and a number of small rounded lobules on posterior and lower edges.

Body scales smooth, midbody scale rows 26–28 ($\bar{x}$ = 26, SD = 0.93, n = 8); paravertebral scales 53–60 ($\bar{x}$ = 56.1, SD = 2.47, n = 8).

Basal scales of third and fourth fingers usually fused to form a single broad scale (69%), occasionally separate; scales on top of fourth finger 7–9 ($\bar{x}$ = 8.1, SD = 0.69, n = 8); lamellae beneath fourth finger 9–13 ($\bar{x}$ = 11.8, SD = 1.67, n = 8); scales on top of fourth toe 11–13 ($\bar{x}$ = 11.0, SD = 1.03, n = 8); lamellae beneath fourth toe 21–28 ($\bar{x}$ = 25.0, SD = 1.98, n = 5), smooth and broad.

Osteology. Premaxillary teeth 11 (n = 2); presacral vertebrae 29; postsacral vertebrae 47–49 ($\bar{x}$ = 47.5, SD = 0.93, n = 4); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively; 2 pairs of ribs contacting mesosternum.

Coloration. Mid to dark brown dorsally and laterally; both dorsal and upper lateral surfaces (including head) with dark markings aligned longitudinally giving the appearance of a series of broken lines the intensity of which varies between individuals but is at least obvious anteriorly; dorsolateral edge with a dark bar between eye and naris, and a lighter dark edged russet stripe (approximately one scale width) between eye and forelimbs, merging with the general body colour posterior of forelimbs; tail unmarked above and with scattered dark markings below, bright orange-reddish in life; ventral surface usually without dark markings, in life with a yellow flush to the chest and abdomen and pink flush to the throat. The holotype has obvious black markings on the throat which are absent from other adult females in the type series.

Figure 2. Paratype of *Sigaloseps ruficauda* n.sp. (AMS R148004), an adult male.

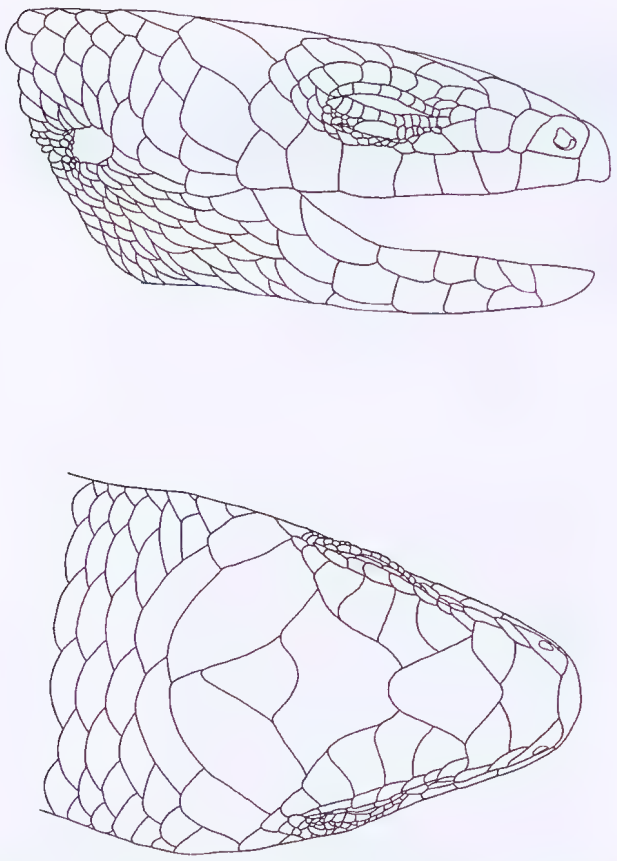

Figure 3. Lateral and dorsal views of the head of holotype of *Sigaloseps ruficauda* n.sp. (AMS R146482).

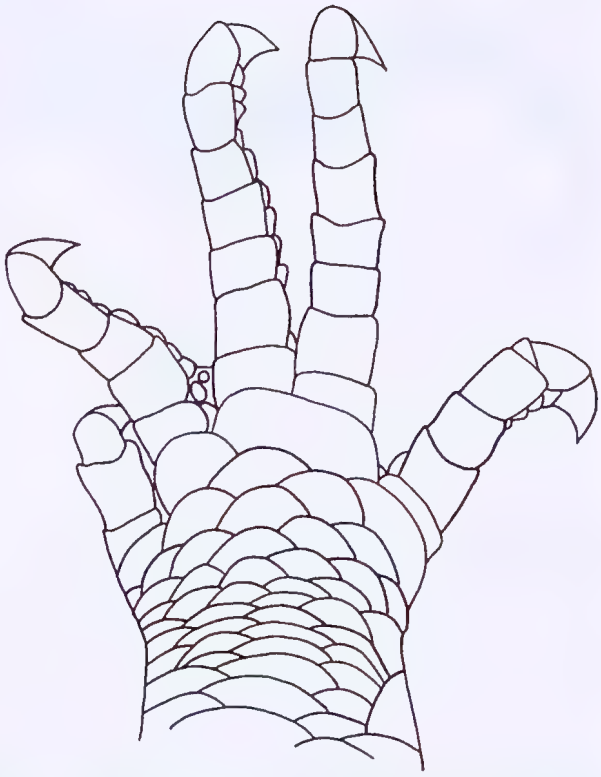

Figure 4. Dorsal view of the hand of *Sigaloseps ruficauda* n.sp. (AMS R146482) showing fusion of basal scales of the third and fourth digits (typical also of *Sigaloseps deplanchei*).

Dorsal surface of the single adult male lighter anteriorly with a dull russet suffusion (including pale dorsolateral edge between the eye and forelimbs), whereas this region tended to be nearly uniform in colour in adult females.

Details of holotype. Adult female; size 56 mm SVL; distance from axilla to groin 31 mm; distance from forelimb to snout 20 mm; hindlimb length 17 mm; tail length 64 mm, reproduced.

Midbody scale rows 26; paravertebral scale rows 58; dorsal scales of fourth finger 9/9; lamellae of fourth finger 13/12; dorsal scales of fourth toe 12/12; lamellae of fourth toe 25/25.

Gravid with 3 (1/2) shelled oviductal eggs.

Distribution. Summits of Mt Ouin (1,100 m asl) and Mt Mou (1,120–1,150 m asl) in southern New Caledonia.

Biology. *Sigaloseps ruficauda* is known only from low closed forest near the summit of Mt Ouin and maquis shrubland adjacent to low closed forest near the summit of Mt Mou.

Maquis is a heathy formation on ultrabasic rocks, it includes 30% of the native species, 36% of the genera, and 47% of the families, 93% of the species are endemic to New Caledonia (Morat *et al.*, 1986). On Mt Mou the high altitude maquis has a dense understorey of ferns. *Sigaloseps ruficauda* was collected among the jumbled rocks covered by the understorey. The environment beneath the rocks was cool and moist. Specimens were also collected from beneath rocks at the interface of the maquis and adjacent closed forest habitat at approximately 1,100 m, here the environment beneath the rocks was also cool and moist. *Sigaloseps ruficauda* was not recorded from the interior of high altitude closed forest on Mt Mou, although this may be due to the limited number of sheltering sites to search. The single Mt Ouin specimen was found under a pile of rocks and wet earth in a track cutting through closed forest.

Two adult females collected on Mt Mou in 16 January were gravid (SVL 48 and 56 mm) and contained 3 shelled oviducal eggs. A clutch of several eggs was found at Mt Mou on 16 January under a small stone beside the track, the young at hatching measured approximately 25–27 mm snout-vent length.

Conservation status. The limited data available indicates *Sigaloseps ruficauda* is restricted to the tops of ranges in the south of the island. Its broader distribution is likely to be as a number of scattered relictual populations between 900–1,200 m altitude. The occurrence of *Sigaloseps ruficauda* at the two known sites appears to be based less on vegetation type than on other variables, such as habitat structure (presence of sheltering sites) and possibly moisture. It is therefore difficult to predict its distribution throughout the region.

Mining activity on the mid to upper slopes of the New Caledonian ranges is most prevalent in the central ranges of the island and on isolated peaks on the west coast. Mining at high altitude in the southern New Caledonia is at present

limited. However, should it be extended to areas where *Sigaloseps ruficauda* is likely to occur, it could have a marked negative impact upon on this and other reptile species restricted to high altitude habitat in the region.

Neither of the known populations of *Sigaloseps ruficauda* are currently protected within a fauna reserve, although the population on Mt Mou is within the Mont Mou Réserve Spéciale Minières et Botanique. Collection and disturbance of minerals and vegetation in this reserve is prohibited, and therefore there is some protection to habitat within the reserve.

Because of the restricted nature of its distribution and apparently restricted habitat preferences *Sigaloseps ruficauda* could conservatively be regarded as Vulnerable:D2 under the current IUCN (1996) classification system (very small population or very restricted distribution; population is susceptible; area of occupancy < 100 km^2 or number of locations < 5). When the fragmented nature of its distribution is also taken into account, any human activity in the region which could threaten its preferred habitat would place this species in a higher category of risk. A further consideration is its known occurrence lies outside of designated fauna reserves.

Field research to further determine the species distribution and habitat preferences (particularly the extent of its reliance upon high altitude maquis habitat) are required before its conservation status and the potential impact of development on the species can be determined with certainty.

Figure 5. Habitat at the type locality for *Sigaloseps ruficauda* n.sp., at approximately 1,100 m asl on Mt Mou, New Caledonia.

Sigaloseps deplanchei (Bavay)

Figs. 4, 6, 7

The description of *Lygosoma deplanchei* by Bavay (1869) lists only a single set of measurements but refers to the species as having been encountered more than once. It was one of eight new scincid lizards described by him from New Caledonia for which no types were designated at the time of description, nor any indication as to where the specimens on which the descriptions were based were lodged.

Boulenger's (1887) account of *Lygosoma deplanchii* listed as material in The Natural History Museum, London (BMNH) two types from New Caledonia presented by Bavay (now registered as BMNH 86.9.16.1-2), and the single type of *Hinulia tetragonurus* Günther. Günther's (1872) description of *Hinulia tetragonurus* is one of four new scincid lizards purportedly obtained from the "Feejee Islands"—all of which are synonymous with New Caledonian species already described by Bavay (see Sadlier 1986: 4, for more detail).

Roux (1913) provided the first comprehensive description of the species based on specimens collected by Roux and Sarasin in 1911–12. This collection (12 specimens are registered in the NHMB) came from two localities on the east coast, Yaté and Ngoi.

Some of Bavay's specimens were recently discovered in the Museum National d'Histoire Naturelle Paris, among them, three syntypes of *Lygosoma deplanchei* Bavay (Brygoo, 1985).

Sadlier (1986) reviewed the species and erected the monotypic genus *Sigaloseps* to accommodate *Lygosoma deplanchei* Bavay. This review was based largely on the specimens collected by Roux and Sarasin, together with the BMNH syntypes of *Lygosoma deplanchei* and *Hinulia tetragonurus*, and five specimens from other sources. Unaware of the recent discovery of several syntypes in the MNHN, Sadlier designated a lectotype for *Lygosoma deplanchei* from one (BMNH 86.9.16.1) of the two BMNH syntypes.

In the past 13 years (1986–1998) more intensive field research has resulted in the acquisition of additional specimens from a broad range of localities. This additional material is the basis for the more detailed description of *Sigaloseps deplanchei* that follows.

Material examined. The redescription of *Sigaloseps deplanchei* (below) is based on the following series of specimens:

West coast and ranges: AMS R144348–49, R144352, R146546–60, 146576–84, R146587 Mt Koghis (500 m) 22°10'S 166°30'E; R135167–69 Yahoué Valley, Nouméa 22°13'S 166°30'E; R147849 Fôret Thy 22°11'S 166°37'E; R78246–47 Mt Dore (eastern base), 2 km W Plum turnoff on Mt Dore road 22°17'S 166°37'E.

Plaine des Lacs region: AMS R125824, R125899, R135609–11 Rivière Bleue, Kaori Géant 22°06'S 166°39'E; R125895 Rivière Bleue, 1 km E Kaori Géant 22°06'S 166°39'E; R147916 Rivière Bleue, Haute Rivière Bleue Walk 22°05'S 166°37'E, R147952–53 Rivière Bleue, 4.7 km E Pont Germain 22°06'S 166°41'E; R147954 Rivière

Figure 6. Records of *Sigaloseps ruficauda* n.sp. (■) and *Sigaloseps deplanchei* (●) in southern New Caledonia.

Bleue, Hoop Géant 22°09'S 166°41'E; R148063–67 Fôret Nord on SW base of Kwa Néie 22°19'S 166°54'E; CAS 158391–92 Mt Aiguillon (= Kwa Néie 22°19'S 166°54'E).

East coast: CAS 157690–91, 158336–42, 162352–53 Goro 22°17'S 167°01'E; NHMB 7198–201, 7205 Yaté 22°09'S 166°55'E.

The following specimens were also examined and are used in compiling the general distribution of *Sigaloseps deplanchei*, but were not used in the redescription (below): AMS R150066 headwaters of Ni River, east of Mt Ouin (745 m) 21°59'S 166°30'E; AIM 1716, 1718, 1730, 1748–49, 1751–52, 1774 Pic Ningua 21°45'S 166°08'E.

Diagnosis. See account for *Sigaloseps ruficauda*.

Description. *Measurements* (adults only): maximum SVL 46 mm; distance from axilla to groin 50–61.1% SVL ($\bar{x}$ = 55.5, n = 57); distance from forelimb to snout 36.8–43.6% SVL ($\bar{x}$ = 39.5, n = 57); hindlimb length 28.6–34.4% SVL ($\bar{x}$ = 31.6, n = 55); tail as long, or slightly shorter or longer than body 87.5–110.8% SVL ($\bar{x}$ = 100.4, n = 21).

Scalation. Frontonasal broader than long; prefrontals narrowly to moderately separated, rarely widely separated; frontal longer than wide; frontoparietals fused; interparietal distinct; parietals each bordered by a nuchal and upper secondary temporal; nuchals occasionally divided to form two smaller equal size scales, and occasionally separated and not contacting medially along the vertebral axis; primary temporal single (93%, n = 64), rarely divided obliquely to form two similar sized scales; upper secondary temporal single and overlapping lower; lower secondary temporal single (98.4%, n = 64), very rarely divided obliquely to form two near similar sized scales; tertiary temporals two; postlabials two; nasals moderately large, usually widely separated; supraciliaries usually seven (87.3%, n = 63), occasionally six; upper labials seven, last very rarely divided by an oblique suture; lower labials six; postmental contacting second lower labial; large chinshields three,

Figure 7. *Sigaloseps deplanchei* from Mt Koghis in southern New Caledonia.

members of first pair in broad contact, members of second pair separated by one scale, members of third pair separated by three scales, all large chin scales flush with lower labials.

Lower eyelid with a large opaque disc centrally (approximately 30% of eye length), which in some individuals is variably divided by one or more transverse sutures to give the appearance of a scaled lower eyelid.

Ear opening moderately large and with 2–4 small acute lobules anteriorly, and a number of small rounded lobules on posterior and lower edges.

Body scales smooth, midbody scale rows 24–28 ($\bar{x}$ = 27.1, SD = 1.43, n = 62); paravertebral scales 46–56 ($\bar{x}$ = 50.6, SD = 2.35, n = 62).

Basal scales of third and fourth fingers usually fused to form a single broad scale (94%), occasionally separate; scales on top of fourth finger (including basal scale) 7–9 ($\bar{x}$ = 7.9, SD = 0.47, n = 58); lamellae beneath fourth finger 10–15 ($\bar{x}$ = 11.9, SD = 0.87, n = 54); scales on top of fourth toe 10–12 ($\bar{x}$ = 11.1, SD = 0.37, n = 59); lamellae beneath fourth toe 24–29 ($\bar{x}$ = 25.9, SD = 1.44, n = 54), broad.

There was no significant difference between the sexes of the largest sample from mid altitude on Mt Koghis (13 males and 12 females respectively) for midbody scale rows ($\bar{x}$ = 27.9 *vs* 28.1, t_{23} = -0.612, P = 0.547), paravertebral scales ($\bar{x}$ = 52.1 *vs* 52.8, t_{23} = -0.906, P = 0.347), scales on top of fourth finger (including basal scale) ($\bar{x}$ = 8.1 *vs* 8.2, t_{23} = -0.853, P = 0.403), lamellae beneath fourth finger($\bar{x}$ = 12.0 *vs* 12.1, t_{22} = -0.230, P = 0.821), scales on top of fourth toe ($\bar{x}$ = 11.3 *vs* 11.0, t_{23} = 1.357, P = 0.188), lamellae beneath fourth toe ($\bar{x}$ = 26.1 *vs* 25.9, t_{23} = 0.386, P = 0.703)

Osteology. Premaxillary teeth 10–11 (n = 2); presacral vertebrae usually 29 (n = 60), occasionally 28 (n = 2) or 30 (n = 3); postsacral vertebrae 35–39 (n = 4); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively (n = 54); 2 pairs of mesosternal ribs contacting mesosternum; atlantal arches fused to the intercentrum.

Coloration. Dorsal surface light to mid-brown, occasionally darker, uniform or variably marked with darker streaks aligned longitudinally to give the appearance of a series of broken lines; lateral surface paler than dorsal, most individuals with a concentration of dark flecks uppermost, tending to be most prominent at the dorsolateral edge of the body; side of head with dark markings, particularly on labial scales and along dorsolateral margin where a dark streak runs from the naris through to near the level of the ear opening; ventral surface yellow posterior to the level of the forelimb and with an orange to pinkish flush to the throat.

There is obvious sexual dimorphism in ventral coloration between adult males and females. Ventral surface of adult males bold yellow posterior to the level of the forelimb, and with a bright orange throat; adult females not so brightly marked, moderate yellow on the abdomen and with a dull pinkish flush to the throat; subadults with no obvious colour to the abdomen and a dull pinkish flush to the throat.

Geographic variation. Across the range of samples geographic variation was observed in seven scalation characters.

There was a trend for samples from the southeast coast at Ngoi (100%, n = 2) and Yaté (83%, n = 6) and from the southeast ranges at Rivière Bleue (78%, n = 9) to have a complete subocular row of scales, whereas those from the Plaine des Lacs region at Kwa Néie (n = 5) and from the west side of the island at or near the Koghis Range (Mt Koghis n = 28, Yahoué Valley, Mt Dore and Fôret Thy collectively n = 8) all had the subocular upper labial contacting the lower eyelid. Samples from Goro (n = 12) on the east coast (only 20 km south of Yaté) are more similar to the adjacent sample at Kwa Néie (10 km east) on the Plaine des Lacs in having the subocular upper labial contacting the lower eyelid.

The same samples were assessed for interpopulation variation in the following six variable scalation characters (see Table 1): midbody scale rows (MBR), paravertebral scales (DSR), fourth finger (FFS) and toe (FTS) scales, and fourth finger (FFL) and toe (FTL) lamellae. There was significant variation in several characters between populations from the southeast coast (Yaté and Goro), the southeast ranges (Rivière Bleue), Plaine des Lacs region (Kwa Néie), or low altitude populations at or near the base of the Koghis range (Yahoué Valley, Mt Dore and Fôret Thy). The sample from Goro had fewer paravertebral scales than the Rivière Bleue (t_{18} = -2.385, P = 0.028) sample; the Yaté sample fewer fourth toe scales than the Rivière Bleue (t_{12} = -2.518, P = 0.027) sample; and the Goro sample more fourth toe scales than the Yaté (t_{13} = 2.404, P = 0.032) sample. There were significant differences between these populations and the mid-altitude population from the Koghis range in midbody scale rows, paravertebral scales, fourth finger scales and lamellae, and fourth toe scales. The Koghis range mid altitude sample had significantly: more midbody scale rows than the Yaté (t_{30} = 4.954, P<0.001), Goro (t_{36} =

7.907, P<0.001), Rivière Bleue (t_{34} = 7.315, P<0.001), or Koghis low altitude (t_{32} = 4.806, P<0.001) samples; more paravertebral scales than the Yaté (t_{30} = 4.247, P<0.001), Goro (t_{36} = 6.114, P<0.001), Kwa Néie (t_{29} = 3.848, P<0.001), Rivière Bleue (t_{34} = 3.377, P<0.002), or Koghis low altitude (t_{32} = 3.787, P<0.001) samples; more fourth finger scales than Goro (t_{34} = 2.163, P = 0.038), Yaté (t_{30} = 4.431, P<0.001), Kwa Néie (t_{29} = 3.529, P<0.001), or Rivière Bleue (t_{34} = 3.535, P<0.001) samples; more fourth toe scales than the Yaté (t_{30} = 2.729, P = 0.011) sample; and more fourth finger lamellae than the Yaté (t_{28} = 2.155, P = 0.040) sample.

The differences in scalation between the low altitude populations at the base of the Koghis range and the regionally sympatric populations on the Koghis range at mid altitude could be viewed in two ways. Firstly as an indication of genetic differentiation between populations at low and high altitude, or as variation in scalation over an altitudinal gradient within a single species i.e., an increase in number of scales with altitude. To further test the first of these possibilities additional high altitude samples from different locations are required. Unfortunately the specimens from high altitude (900–1,000 m asl) at Pic Ningua are from formalin-based pit-fall trap samples and their state of preservation is such that the characters cannot be assessed accurately. To test the second possibility would require samples from the Koghis range at intermediate altitudes between 300 m and 700 m asl.

Distribution. Southern third of New Caledonia to as far north as Pic Ningua (21°45'S 166°08'E), approximately 16 km northeast of the town of Bouloupari. The single specimen of *Sigaloseps deplanchei* collected from the headwaters of Ni River, east of Mt Ouin at mid to high altitude (745 m) is the geographically closest site to the Mt Ouin location for *S. ruficauda*.

Biology. *Sigaloseps deplanchei* occurs in lowland and mid (500 m) to high altitude (1,000+ m) closed forest habitat where it can be relatively abundant. It is a secretive species usually found sheltering beneath rocks, logs, and debris on the forest floor but is occasionally observed active in leaf litter. When active it moves constantly amongst the litter and was not observed to actively bask in sunlit patches.

Gravid females have been collected during the summer (wet season) month of December. Modal clutch size is two, with three eggs recorded occasionally. A sample of six adult females collected on Mt Koghis (500 m asl) in December 1986 had two (n = 5) to three (n = 1) oviductal eggs, whereas a sample of 10 adult females from the same location collected in January 1995 had flaccid oviducts (n = 9) indicating egg laying had occurred, or yolked ovarian follicles (n = 1).

Conservation status. *Sigaloseps deplanchei* is known from over ten sites scattered over much of the ultramafic area in southern New Caledonia. It was previously assessed as moderately widespread and common by Bauer & Sadlier (1993) based on the number of museum specimen records available at that time. It has since been recorded from several additional localities, most notably Pic Ningua which represents a significant range extension to the north, indicating the species is likely to be more widespread in the southern ultramafic region of the island than previous records indicated.

At Mt Koghis, which has been visited repeatedly, *Sigaloseps deplanchei* is common in mid-altitude (500 m asl) closed forest habitat; it has also been collected on successive occasions at several other sites (Goro, Kwa Néie, Rivière Bleue). Because of its moderately widespread distribution *Sigaloseps deplanchei* is considered secure at the island level, and would be regarded as Lower Risk:lc under the current IUCN classification system (1986). However, because it is restricted to closed forest habitat, populations of *S. deplanchei* in the more highly developed west coast lowlands are likely to be threatened at a local level by human activities in these areas.

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Table 1. Variation in scalation characteristics for *Sigaloseps deplanchei* from six locations throughout the species range.

		MBR	DSR	FFS	FFL	FTS	FTL
Yaté	range	26–28	47–51	7–8	10–12	10–11	23–26
	$\bar{x}$	26.4	48.8	7.4	11.2	10.6	24.9
	SD	0.89	1.89	0.55	0.76	0.42	1.89
	n	5	5	5	5	5	4
Goro	range	24–28	46–51	7–8	10–12	10–12	22–28
	$\bar{x}$	26.0	48.4	7.9	11.8	11.0	25.8
	SD	0.89	2.01	0.33	0.76	0.24	1.85
	n	11	11	9	7	10	8
Kwa Néie	range	26	47–51	7–8	11–13	11–12	25–27
	$\bar{x}$	26.0	49.8	7.5	12.0	11.1	25.9
	SD	0.0	1.71	0.58	0.71	0.25	0.75
	n	4	4	4	4	4	4
Rivière Bleue	range	26–28	48–52	6–8	11–14	11–12	25–28
	$\bar{x}$	26.2	50.2	7.6	11.9	11.1	26.4
	SD	0.67	1.30	0.6	0.81	0.33	1.28
	n	9	9	9	9	9	7
Mt Koghis Range	range	26–30	49–55	8–9	11–15	10–12	23–29
(mid altitude)	$\bar{x}$	28.0	52.4	8.2	12.2	11.2	26.1
	SD	0.62	1.78	0.30	0.93	0.41	1.48
	n	27	27	27	25	27	26
Mt Koghis Range	range	26–28	48–51	7–8	10–13	10–11	25–27
(low altitude)	$\bar{x}$	27.6	49.7	7.9	11.2	10.9	25.4
	SD	0.98	1.11	0.38	0.76	0.38	0.65
	n	7	7	7	7	7	5

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The Scincid Lizard *Lioscincus tillieri* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: New Information on the Species' Biology, Distribution and Morphology

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ABSTRACT. *Lioscincus tillieri* was originally described in 1991 from a single juvenile specimen. Field observations on the species at several localities and the acquisition of a further fifteen specimens collected between 1995 and 1998 have provided new data on its biology, distribution, and morphology. Most notably *L. tillieri* is now known to have a live-bearing mode of reproduction, only the second occurrence of viviparity in the endemic New Caledonian skink fauna.

SADLIER, ROSS A., & AARON M. BAUER, 1999. The scincid lizard *Lioscincus tillieri* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: new information on the species' biology, distribution and morphology. *Records of the Australian Museum* 51(1): 93–98.

The New Caledonian scincid lizard *Leiolopisma tillieri* was described by Ineich & Sadlier (1991) from a single specimen collected by entomologists in a malais trap set in Parc Rivière Bleue in the Plaine des Lacs region in the south of the island. The specimen was small (snout to vent length 29.5 mm) and presumed to be a juvenile.

At the time of description it was not possible to unambiguously assign the species to any existing monophyletic genus in the *Eugongylus* group of skinks (Greer, 1979). For this reason it was placed in "*Leiolopisma*" which comprised an essentially primitive assemblage of species from Australia, New Zealand, New Caledonia, and Mauritius (where the type species *Leiolopisma telfairi* occurs on Round Island). In the past 10 years there has been a progressive dismantling of the polyphyletic genus *Leiolopisma* (see Hutchinson *et al.*, 1990). The New Caledonian species placed in *Leiolopisma* by Sadlier (1986) have subsequently been reallocated to *Lioscincus* (Bauer & Sadlier, 1993), the next available generic name to accommodate these taxa. As it currently stands *Lioscincus* includes: *L. greeri, L. maruia, L. nigrofasciolatum, L. novaecaledoniae, L. steindachneri* (type species), and *L. tillieri*, but still remains an assemblage of generally primitive *Eugongylus* group species.

In overall morphology *L. tillieri* is most similar to the recently described New Caledonian species *Lioscincus*

maruia Sadlier *et al.* (1998) and the species of *Tropidoscincus* (also from New Caledonia), most significantly in also having an extremely long tail with 60 or more postsacral vertebrae. However both *L. tillieri* and *L. maruia* lack the unusual skeletal character in the region of the mesosternum that characterises *Tropidoscincus* (as defined by Sadlier, 1986), i.e. the species of *Tropidoscincus* have three mesosternal ribs whereas *L. tillieri* has two, the latter being the primitive character state for the *Eugongylus* group.

Known only from the single juvenile specimen collected in 1991, *Lioscincus tillieri* was listed as rare by Bauer & Sadlier (1993) in an assessment of the distribution and status of the endemic lizards of New Caledonia. The species was not collected again until 1995 when it was located in maquis shrubland on Mt Mou and Mt Vulcain during the course of two periods of field research that traversed that habitat type. Since then it has been located at a further three locations in the south of the island, always in maquis shrubland. The information presented here is a compilation of both opportunistic, and more recently, targeted field research carried out over a number of years. The acquisition of additional specimens has provided data on variation in scalation and osteology, colour pattern in adults, and reproductive mode, all previously unreported.

Materials and methods

Specimen abbreviations are prefixed as follows: Australian Museum (AMS); California Academy of Sciences (CAS); Museum National d'Histoire Naturelle Paris (MNHN).

Measurements. The following characters were scored for each specimen where possible: snout to vent length (SVL)—measured from tip of snout to caudal edge of anal scales; axilla to groin distance—measured from middle of base of the forelimb to middle of base of hindlimb; forelimb to snout length—measured from tip of snout to middle of base of forelimb; hindlimb length—measured from middle of base of hindlimb to tip of fourth toe including nail; tail length—measured from caudal edge of anal scales to tip of tail, on complete original tails only. Body measurements are for adults only, as determined by reproductive maturity (presence of enlarged, yolked ovarian follicles or embryos in females and enlarged testes in males) and/or obvious size classes, and are expressed as percentages of snout to vent length in the taxon accounts.

Scalation. Head scalation generally follows Taylor (1935) as described and figured by Sadlier (1986); midbody scale rows—number of longitudinal scale rows around body counted midway between fore and hindlimb; paravertebral scales—number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at level of vent opening; fourth finger and toe scales—number of dorsal scales on fourth digit of hand and foot, distal scale contains claw and basal scale broadly contacts adjacent basal scale of third finger or toe; fourth finger and toe lamellae—number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale to a point level with intersection of third and fourth digits. Bilateral characters were scored on both sides and the mean value used.

Osteology. Specimens were *X*-rayed to assess phalangeal formula, and the number of presacral and postsacral vertebrae.

Species account

Lioscincus tillieri (Ineich & Sadlier)

Figs. 1–4

Leiolopisma tillieri Ineich & Sadlier, 1991: 343.

Material examined. AMS R148032–33 Mt Vulcain, Mine Galliéni 21°54'S 166°20'E (500 m); AMS R148035–38 Mt Vulcain, vicinity Refuge du Vulcain 21°54'S 166°23'E (970 m); AMS R146479 Mt Mou, 22°04'01"S 166°20'34"E (1,000–1,050 m); AMS R146486 Mt Mou 22°03'53"S 166°20'36"E (1,095 m); MNHN 1989.26 (holotype *Leiolopisma tillieri*), Rivière Bleue, 22°06'05"S 166°40'06"E (310 m); AMS R147909, R152616, R152628, CAS 205462 Rivière Bleue, 22°05'47"S 166°40'13"E; AMS R151335 Yaté (vicinity), 22°10'02"S 166°53'50"E (330 m).

Diagnosis. *Lioscincus tillieri* is distinguished from other species of *Lioscincus* by the following combination of characters: (*a*) scales of dorsal surface of body and tail with two strong keels; (*b*) midbody scale rows 34–38; (*c*) paravertebral scales 65–71; (*d*) lamellae under the fourth finger 18–23; (*e*) lamellae under the fourth toe 27–33; (*f*) parietals each bordered by a nuchal scale and 2 upper secondary temporal scales; (*g*) dorsal surface of head with a relatively unmarked uniform brown colour pattern.

Description. The description is based on 16 specimens comprising nine adults (three males and six females) 52–64 mm SVL, two subadults 41–45 mm SVL, and five juveniles 29.5–38 mm SVL (including the holotype). Measurements are for adults only (n = 9 unless otherwise stated); scalation was assessed on all specimens unless otherwise stated.

Measurements. Distance from axilla to groin 55.9–60.0% SVL;($\bar{x}$ = 57.6); distance from forelimb to snout 36.1–40.0% SVL ($\bar{x}$ = 38.0); hindlimb length 43.8–50.9% SVL ($\bar{x}$ = 47.4); tail 279.2–296.4% SVL ($\bar{x}$ = 288.6, n = 3).

Scalation. Frontonasal broader than long (W/L = 120–140%, $\bar{x}$ = 128.3, n = 6); prefrontals moderately large, narrowly separated (56.25%), in point to narrow contact (25.0%), rarely more widely separated (12.5%) or contacting (6.25%); frontal longer than wide (W/L = 70.5–86.6%, $\bar{x}$ = 78.5, n = 6), the holotype has the frontal fused to the frontoparietals; frontoparietals fused; interparietal distinct; parietals each bordered by a nuchal scale and two, rarely one, (6.2%) upper secondary temporal scales; primary temporal single; lower secondary temporal single; tertiary temporals usually two, occasionally three (9.4%); postlabials two; nasals moderately to widely separated; supraciliaries 4–7, usually 5 (34.4%) or 6 (56.2%), rarely 4 or 7, third usually elongate and bordering posterior half of first supraocular and nearly all of second supraocular; upper labials 7, rarely 6 (4.1%); lower labials 6, rarely 5 (4.1%); postmental contacting first and second lower labial; chinshields three, first pair in broad medial contact.

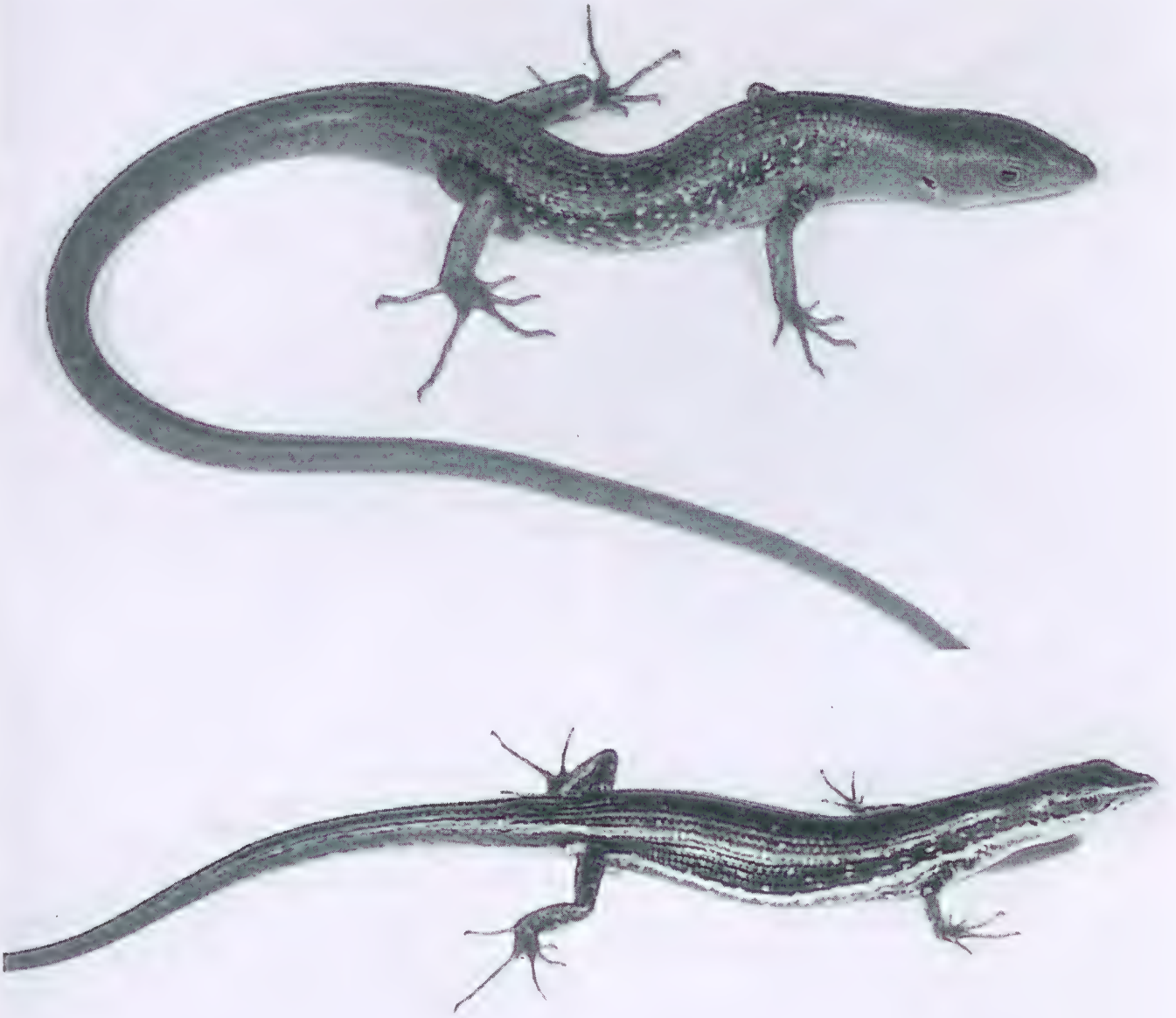

Figure 1. Male (upper) and female (lower) of *Lioscincus tillieri*.

Lower eyelid with an obvious semi-transparent disc, length approximately 33–38.5% ($\bar{x}$ = 36.4, n = 6) of total eye length.

Ear opening moderately large and with enlarged lobules anteriorly.

Scales of body and tail with two strong keels; midbody scale rows 34–38 ($\bar{x}$ = 35.1, SD = 1.23, n = 16); paravertebral scales 65–71 ($\bar{x}$ = 68.3, SD = 1.85, n = 16); scales on top of fourth finger 15–18 ($\bar{x}$ = 17.1, SD = 0.51, n = 16); lamellae beneath fourth finger 18–23 ($\bar{x}$ = 20.3, SD = 1.00, n = 16); scales on top of fourth toe 21–25 ($\bar{x}$ = 22.6, SD = 1.07, n = 16); lamellae beneath fourth toe 27–33 ($\bar{x}$ = 30.5, SD = 1.76, n = 16), smooth.

Osteology. Premaxillary teeth (adults only) 9 (n = 4), or 11 (n = 1); presacral vertebrae 28–29 ($\bar{x}$ = 28.9, SD = 0.34, n = 16); postsacral vertebrae 58–73 ($\bar{x}$ = 64.9, SD = 5.52, n = 7); phalangeal formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively; two pairs of ribs contacting mesosternum.

Coloration. There is sexual dimorphism in colour and pattern between the three adult males and six adult females. Adult females are more obviously two-toned having contrasting light dorsal and dark lateral coloration, and have a pale hip-stripe along the dorsolateral margin which is absent in males.

Adult males (Fig. 1, upper): dorsal surface brown with scattered light and dark markings, lighter in colour overall than females and with the differences in tone between the dorsal and lateral colours not as pronounced as in females. Dorsal markings aligned as in females to resemble obscure dark-edged ocelli. No pale hip stripe along posterior dorsolateral edge. Head a uniform brown above and at the sides. Lateral surface distinct from dorsal surface, two-toned between fore and hindlimbs being black uppermost and

Figure 2. Distribution of *Lioscincus tillieri* in New Caledonia, specimen records (●) and observation records (O).

midbrown below with variable pale spotting overall, pale midlateral stripe obscure, most obvious just behind forelimb. Ventral surface in life, bold lemon yellow.

Adult females (Fig. 1, lower): dorsal surface brown (some individuals darker or lighter in tone) and either relatively uniform (smaller adult females) or with variable light and dark markings in which the dark flecks are aligned along the anterior and posterior edge of the pale spots to give the overall appearance of obscure, pale, dark-edged ocelli in the most boldly marked of the females. Posterior dorsolateral edge in region of hindlimbs with a narrow (1 scale width) pale hip stripe, covering the basal portion of the tail and area in front of hindlimbs, poorly expressed in two smaller adult females. Lateral surface dark brown-black, distinct from dorsal, with variable pale spotting uppermost and prominent pale midlateral strip (1 scale width). Ventral surface in life, bold lemon yellow.

Distribution. *Lioscincus tillieri* appears to be endemic to maquis habitat in the ultramafic block that covers much of the southern third of the island. Maquis is a heathy formation on ultrabasic rocks, it includes 30% of the native species, 36% of the genera, and 47% of the families occurring in New Caledonia. Ninety-three percent of the species are endemic to New Caledonia (Morat *et al.*, 1986). Within this region (Fig. 2) *L. tillieri* has been recorded from Mt Vulcain in the north to Kwa Néie in the south. Specimen based records are from Mt Vulcain, Mt Mou, Rivière Bleue, and Yaté, and observations from Montagne des Sources and Kwa Néie. It occurs over a broad altitudinal range from low (200 m asl) to high (1,000 m asl) elevation.

Biology. During the course of several visits to New Caledonia observations were made on *Lioscincus tillieri* at Mt Mou (January and September 1995), Mt Vulcain (September 1995), and the type locality of Parc Rivière Bleue (September 1995 and May 1998). The habitat at all three locations is maquis heathland, with notable differences between each site. High elevation maquis at Mt Mou is low and dense with an impenetrable understorey of ferns (Fig. 3). By contrast, the mid to high altitude maquis at Mt Vulcain (700–900 m asl) is low and open (Fig. 4). Low altitude maquis (250 m asl) at Rivière Bleue is well developed and lies adjacent to a forest of *Casuarina* with a dense and tall (1 m) grassy understorey—several *Lioscincus tillieri* were observed at the ecotone between the two habitats.

Both adults and juvenile *Lioscincus tillieri* were observed on the ground amongst shrubs and grasses, and occasionally perched on the groundcover. Clearly arboreal habits were observed on several occasions: an adult male was seen on the trunk of a sapling oriented head down and clearly trying to keep itself pressed flat against the trunk (AMB); one

individual was sighted in a low bush and dropped to the ground when disturbed; and two others not initially seen perching dropped to the ground from a low bush when disturbed. On all occasions *L. tillieri* was wary and difficult to approach. In particular juveniles and subadults observed in elevated positions were only seen briefly before dropping to the ground and seeking shelter. The type specimen of the species was a juvenile collected by entomologists in a malais trap approximately 1 m above the ground.

There are few sheltering sites in maquis habitat. The only specimen of *Lioscincus tillieri* located by searching beneath ground cover was a single individual from Col d'Yaté collected under a stone during overcast and showery weather (A. Whitaker, pers. obs.).

The records of viviparity for the species are from two adult females collected on Mt Mou in January (SVL 60.5 mm and 64 mm) which contain embryos with all scalation features obvious. Three adult females collected in September (SVL 52–55 mm) contained 2–3 large oviductal eggs. This is only the second case of viviparity recorded in the New Caledonian skinks, the other live-bearing species being *Marmorosphax tricolor* (Sadlier, 1986).

Conservation status. *Lioscincus tillieri* is known from six locations and under optimal conditions was observed to be moderately common at two of these (Mt Vulcain and Rivière Bleue). For these reasons it is regarded as only moderately restricted in distribution and is not considered to be rare, and would not be regarded as threatened under the current IUCN classification system (1996).

Our field research clearly indicates that *Lioscincus tillieri* is restricted to maquis habitat, and that it inhabits structurally different types of maquis. However, it is not known whether any particular successional stage of maquis is preferred. Consequently the impact of fire and disturbance by mining on maquis habitat are unknown but could be significant and impact on populations of *L. tillieri* at a local level. Field research in the maquis shrublands of the southern ultramafic block is required to clearly establish the species' habitat requirements in order to fully assess the species conservation status.

Figure 3. Maquis habitat at Mt Mou (800+ m asl).

Discussion

Relationships. *Lioscincus* is an assemblage of generally primitive *Eugongylus* group species from New Caledonia that can not be assigned to any existing monophyletic genus. The species included in the genus possess the following basic suite of derived characters: supranasal scale absent; frontoparietals fused to form a single scale; lower eyelid with a semi-transparent disc; presacral vertebrae 29. *Lioscincus tillieri* clearly possesses a larger suite of apomorphic character states, most notably the presence of two strong keels to the scales of the dorsal surface of the body and tail, and a viviparous mode of reproduction. Its inclusion in *Lioscincus* is considered temporary pending further research on the relationships of these species.

Aside from *Lioscincus tillieri* five other species of New Caledonian skinks have the derived character state of an extremely long tail. Three species of *Tropidoscincus*, the monotypic *Lacertoides pardalis*, and the recently described *Lioscincus maruia*, all have tails as much as 2.5 times longer than the body and an exceptionally high number of postsacral vertebrae, usually 60 or more. It is possible that this common feature is indicative of close relationship between these species. It is also interesting to note that they all inhabit open forest or shrubland habitats, although *Tropidoscincus variabile* and *T. rohssii* also occur in open areas within closed forest habitat.

Lioscincus tillieri is most similar to *L. maruia* in body proportions (long-limbed and long-tailed), habits and habitats (surface active species inhabiting maquis shrubland), and certain aspects of scalation (keeled body scales), osteology ($\bar{x}$ = 58 postsacral vertebrae), and coloration (yellow flush to the ventral surface). However *L. maruia* differs from *L. tillieri* in a number of aspects, most notably in having: weakly tricarinate *vs* strongly bicarinate body and tail scales; modally 11 *vs* 9 premaxillary teeth; a single upper secondary temporal scale *vs* two; and an oviparous *vs* viviparous mode of reproduction. For these characters the condition described for *L. tillieri* is most likely the apomorphic state. In any case they serve to further diagnose the species and emphasis its uniqueness.

Figure 4. Maquis habitat at Mt Vulcain (950 m asl).

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Pacific Tanaidacea (Crustacea): Revision of the Genus *Agathotanais* with Description of Three New Species

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ABSTRACT. New Pacific material of the cosmopolitan genus *Agathotanais* Hansen, 1913 has made a generic revision possible. Newly discovered character states for the antenna have made it necessary to modify the generic diagnosis. Three new species—*A. manganicus* and *A. ahyongi* from the central Pacific and *A. spinipoda* from the continental shelf and slope off southeastern Australia–are described, they increase the number of species in the genus to eight. A key to the females of *Agathotanais* species is provided. Sexual dimorphism is generally restricted to the presence of pleopods in the male. The characters defining *Agathotanais* are considered apomorphic within the Tanaidomorpha. The distribution pattern of *Agathotanais* is discussed.

LARSEN, KIM, 1999. Pacific Tanaidacea (Crustacea): revision of the genus *Agathotanais* with description of three new species. *Records of the Australian Museum* 51(2): 99–112.

The vast abyssal plain of the Pacific Ocean is practically unexplored. Within the Pacific, the Australian region represents an area of particular interest since Australia was the last landmass to separate from Antarctica. The Australian crustacean fauna is considered both archaic and diverse (Poore & Wilson, 1993). The southern region of Australia contains elements derived from the Tertiary circumpolar Weddellian fauna (Poore, 1994). Because of the long period of isolation, Australia has a high degree of endemicity (e.g., about 90% for isopod crustaceans, N.L. Bruce, pers. comm.). This region has, therefore, the greatest potential for discovery of new invertebrates (Poore *et al.*, 1994).

Hansen erected the genus *Agathotanais* in 1913 for the species *Agathotanais ingolfi*. The latter is found in large numbers throughout the deep North Atlantic (Hansen, 1913; Lang, 1971b; Bird & Holdich, 1988; Larsen, in press). Subsequently, four closely related species have been described. *Agathotanais splendius* Kudinova-Pasternak, 1970 from the northwest Pacific (2 specimens), *A. hanseni* Lang, 1971b from the Central American Pacific slope (5 specimens), *A. ghilarovi* Kudinova-Pasternak, 1989 from the Indian Ocean (29 specimens) and *A. brevis* Kudinova-Pasternak, 1990 from the South Atlantic (1 specimen). The genus is represented in all oceanic regions of the world.

Materials and methods

Types and other specimens of *Agathotanais manganicus* n.sp. and *A. ahyongi* n.sp. are deposited at the Australian Museum (AM). Types and other specimens of *A. spinipoda* n.sp. are in the Museum of Victoria (MV), Melbourne. Paratypes of *A. hanseni* are deposited in the American Museum of Natural History (AMNH), New York. Paratypes of *A. ingolfi* are located in the Zoological Museum of the University of Copenhagen (ZMUC), Denmark. Types of *A. splendius, A. brevis* and *A. ghilarovi* are located in the Moscow State University Museum (MSU), Russia.

Station data are given in Table 1. DOMES (Deep Ocean Mining Environmental Study) data were collected by G.D.F. Wilson & party on *RV Oceanographer*—sampler: Sandia 0.25 m^2 box core. Station list data for other "DOMES site A" stations are given in Thistle & Wilson (1987). Slope data were collected by G.C.B. Poore & party and M.F. Gomon & party on *RV Franklin*—sampler: epibenthic sled; station list and data for other "slope" stations are given in Kornicker & Poore (1996).

Table 1. Station list: DOMES (Deep Ocean Mining Environmental Study) site A; Clipperton and Clarion fracture zone; equatorial Pacific abyssal plain. Slope stations: southeastern Australian shelf.

DOMES #1	station DJ02	09°23.52'N	151°32.94'W	5155 m	23 Nov 1977
DOMES #1	station DJ15	09°20.30'N	151°24.10'W	5166 m	26 Nov 1977
DOMES #1	station DJ20	09°19.80'N	151°35.10'W	5260 m	27 Nov 1977
DOMES #1	station DJ23	09°33.23'N	151°38.33'W	4934 m	28 Nov 1977
DOMES #1	station DJ38	09°36.30'N	151°58.00'W	5086 m	03 Dec 1977
DOMES #2	station DJ41	09°22.70'N	151°28.00'W	5191 m	18 May 1978
DOMES #2	station DJ50	09°22.10'N	151°58.00'W	5086 m	20 May 1978
DOMES #2	station DJ66	09°27.00'N	151°35.90'W	5250 m	25 May 1978
DOMES #2	station DJ69	09°15.80'N	151°30.70'W	5049 m	25 May 1978
DOMES #2	station DJ72	09°33.80'N	151°21.30'W	5240 m	27 May 1978
DOMES #2	station DJ73	09°28.10'N	151°15.60'W	5107 m	27 May 1978
DOMES #2	station DJ77	09°21.30'N	151°21.50'W	5034 m	28 May 1978
slope	station 27	38°25.00'S	149°00.00'E	1500 m	22 Jul 1986
slope	station 32	38°21.90'S	149°20.00'E	1000 m	23 Jul 1986
slope	station 33	38°19.60'S	149°24.30'E	930 m	23 Jul 1986
slope	station 40	38°17.70'S	149°11.30'E	400 m	24 Jul 1986
slope	station 53	34°52.72'S	151°15.04'E	996 m	22 Oct 1988
slope	station 67	38°23.95'S	149°17.02'E	1277 m	25 Oct 1988
slope	station 69	38°29.33'S	149°19.98'E	1840 m	26 Oct 1988

Systematics

Suborder Tanaidomorpha Sieg, 1980
Superfamily Paratanoidea Lang, 1949
Family Anarthruridae Lang, 1971a
Subfamily Anarthrurinae Lang, 1971a
Tribe Agathotanaini Lang, 1971a

Genus *Agathotanais* Hansen, 1913

Synonymy. *Agathotanais* Hansen, 1913, 3(3): 8, 63, 64.–Nierstrasz, 1913, 32a: 38.–Barnard, 1920, 17: 331.–Zimmer, 1926, 3(1): 686, 690, 696.–Lang, 1949, 42(18): 7.–Shiino, 1952, 2(2): 63.–Beklemischew, 1958, 1: 268, 298.–Lang, 1968, 1: 160.–Kudinova-Pasternak, 1970, 86: 370.–Lang, 1971a, 21: 57–59.–Lang, 1971b, 23: 363–365.–Sieg, 1973, 33: 282.–Gardiner, 1975, 170: 179.–Sieg, 1976, 14: 178.–Bird & Holdich, 1988, 22: 1592, 1597.–Bird & Holdich, 1989, 23: 137.–Kudinova-Pasternak, 1990, 126: 100.

Diagnosis (modified after Hansen, 1913; Lang, 1971b and Bird & Holdich, 1988): cuticle heavily calcified and deeply pitted. Antennule with 3 articles. Pleon narrower than pereon and pleotelson. Antenna greatly reduced, more so in female than male. Mandible molar process consisting of membranous lobe only. Left mandible lacina mobilis absent or reduced to knoblike process fused with incisor. Maxillule endite with 7–11 spines. Labium with anterolateral processes and mostly with medial plumose setae. Maxilliped endites circular or hexagonal. Except for the distal part of cheliped and pereopod dactylus, all appendages setulose. Chelipeds slender, attached to cephalothorax ventrally and not via carapal sclerite. Pereopods 4–6 dactylus and terminal spine not fused. Uropods short, stout, uniramous and uniarticulate.

Type species: *Agathotanais ingolfi* Hansen, 1913

Gender: masculine.

Remarks. *Agathotanais* is unique within the Tanaidomorpha because of the reduced antenna. Within the Anarthruridae, no other genera display even remotely similar reductions although both the *Paranarthrura* and *Paragathotanais* share some generic features.

Agathotanais splendius and *A. brevis* are incompletely described from few specimens. Specimens of these species could not be obtained for revision. The validity of these species is therefore uncertain.

The status of *A. hanseni* is similarly problematic. Lang (1971b) did not illustrate the diagnostic characters in his description of this species. The holotype is apparently lost (as well as that of *A. ingolfi*) and the paratypes are all in poor condition. One specimen of *A. hanseni* was reported from the Atlantic near the Azores (Lang, 1971b). This specimen, however, could not be located and, considering the identification problems associated with tanaids, the Atlantic record may be a misidentification. Lang (1971b) stated that *A. ingolfi* could be distinguished from *A. hanseni* by the following characters: (*a*) width/length ratio of pereonite 4–5, greater in *A. ingolfi* (P4 = 1.0, P5 = 1.1) than *A. hanseni* (P4 = 0.78, P5 = 0.85); (*b*) anterolateral carapace margins convex for *A. hanseni* and concave for *A. ingolfi*; (*c*) eleven heavy setae on the maxillule of *A. hanseni*, while 10 in *A. ingolfi*. Some specimens in the Northwest Atlantic, however, had convex anterolateral margins (*A. hanseni* character) and a width/length ratio of P4 = 1.0, P5 = 1.05 corresponding to that of *A. ingolfi* (Larsen, in press). The *A. hanseni* paratypes specimens have suffered various degrees of air-drying. They appear to have shrunk in width rather than length thus obscuring this character. Little confirmation is gained from examining the shape of the carapace on the paratypes, because two specimens lack the head altogether and another is male (the males of the two species shows no morphological differences). On the two complete female specimens, the anterior corners of the carapace are convex. The stout setae on the maxillule are not a reliable taxonomic character because they are known to be ontogenetically dependent (Larsen & Wilson, 1998) and are also inconspicuous in the two species (Bird & Holdich, 1988: 1598). The latter authors also suggest caution regarding this character.

Kudinova-Pasternak (1989) illustrates the pleopod as belonging to the female and the mandibles as belonging to the male for *A. ghilarovi*. This, however, is an editorial mistake and the text describe these, correctly, as male pleopods and female mandibles.

Agathotanais manganicus n.sp.

Material examined. HOLOTYPE (AM): 1 ovigerous ♀, DOMES site A, station DJ 23, (body length = 2.9 mm), AM P51003. PARATYPES (AM): 1 nonovigerous ♀, DOMES site A station DJ20, mouthparts and limbs dissected, AM P50999; 1 nonovigerous ♀, DOMES site A station DJ02, cut in two, mounted on SEM stub and coated, AM P50997.

Other material. 1 fragmented ♀, 2 mancas, DOMES site A station DJ23; 1 nonovigerous ♀ (fragmented), DOMES site A station DJ50; 1 ovigerous ♀, DOMES site A station DJ66; 1 juvenile ♀, DOMES site A station DJ72.

Diagnosis of female. Antennule article 1 longer than all distal articles together, antenna with 2 articles, longer than 0.5 length of antennule first article. Pereonite 6 longer than broad.

Etymology. Name refers to the Manganese Nodule Province where the specimens were collected.

Description of adult female (Fig. 1A,B). *Body* cylindrical, slender. *Cephalothorax* (Fig. 1C) shorter than first 2 pereonites combined, anterolateral corners slightly concave. *Pereonites* tapering posteriorly, pereopod shoulders placed anteriorly on pereonites 1–3, about midlength on pereonite 4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long (l/w ratio 0.8), shorter than all other pereonites. *Pereonite 2–6* l/w ratios 1.0, 1.15, 1.5, 1.5, 1.1 respectively. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* as long as last 3 pleonites together, apex margin straight. *Antennule* (Fig. 1M) with 3 articles. *Article 1* longer than rest of antennule, with 1 simple seta midlength and 1 distally. *Article 2* less than 0.25 times article 1 length, with 1 simple seta distally. *Article 3* 0.4 times longer than article 2, cone shaped with 5 simple setae and 1 aesthetasc distally. *Antenna* (Fig. 1N) 2-articulate, longer than 0.5 length of antennule first article, with 2 distal simple setae. *Mouthparts*. *Labrum* (Fig. 1D), distal margin rather flat, setose. *Mandibles*, molar process consisting of only a membranous lobe. *Left mandible* (Fig. 1E) lower part of incisor pointed; lacina mobilis absent. *Right mandible* (Fig. 1F), incisor bifurcate, upper part pointed, lower part blunt. *Maxillule* (Fig. 1H) endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 1I) elongated without recognisable features. *Labium* (Fig. 1J) with anterolateral processes and a plumose spiniform seta midlength. *Maxilliped* (Fig. 1K) basis fused medially. Endite hexagonal, not fused medially and more heavily setose on anterolateral corners. Palp article 1 outer margin longer than inner, smooth; article 2 inner margin longer than outer and with 3 distal setulate setae; article 3 with 3 setulate setae on inner margin; article 4 with 5 distal setulate setae. *Epignath* (Fig. 1L) with distal setules. *Cheliped* (Fig. 2G). *Basis* quadrate, half the length of carpus. *Merus* with 1 simple setae sternally. *Carpus*, about as long as propodus, with 2 simple setae at midlength on sternal margin. *Propodus* (Fig. 2H) with 1 simple seta medially on sternal margin and 1 by dactylus insertion. *Fixed finger* with 3 distal setae on inner margin; distal tooth bifurcate. *Dactylus* with small process by insertion of distal tooth. *Oostegites* (Fig. 1G) originating from pereonite 1–4. Anterior margin of oostegite 1 with scattered setules. *Pereopod 1* (Fig. 2A). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* with 1 distal simple seta on each margin. *Merus* expanding in width distal, half as long as carpus, with 1 distal simple seta on tergal margin. *Carpus* as long as dactylus and terminal spine together, with 1 simple seta on tergal margin and 1 medial on distal margin. *Propodus* 0.25 times longer than carpus, with 1 simple long seta and 2 distal short setae. *Dactylus* and terminal spine shorter than propodus. *Pereopod 2* (Fig. 2B) similar to pereopod 1 except *basis* with 1 seta near midlength on sternal margin; *ischium* smooth; *carpus* with

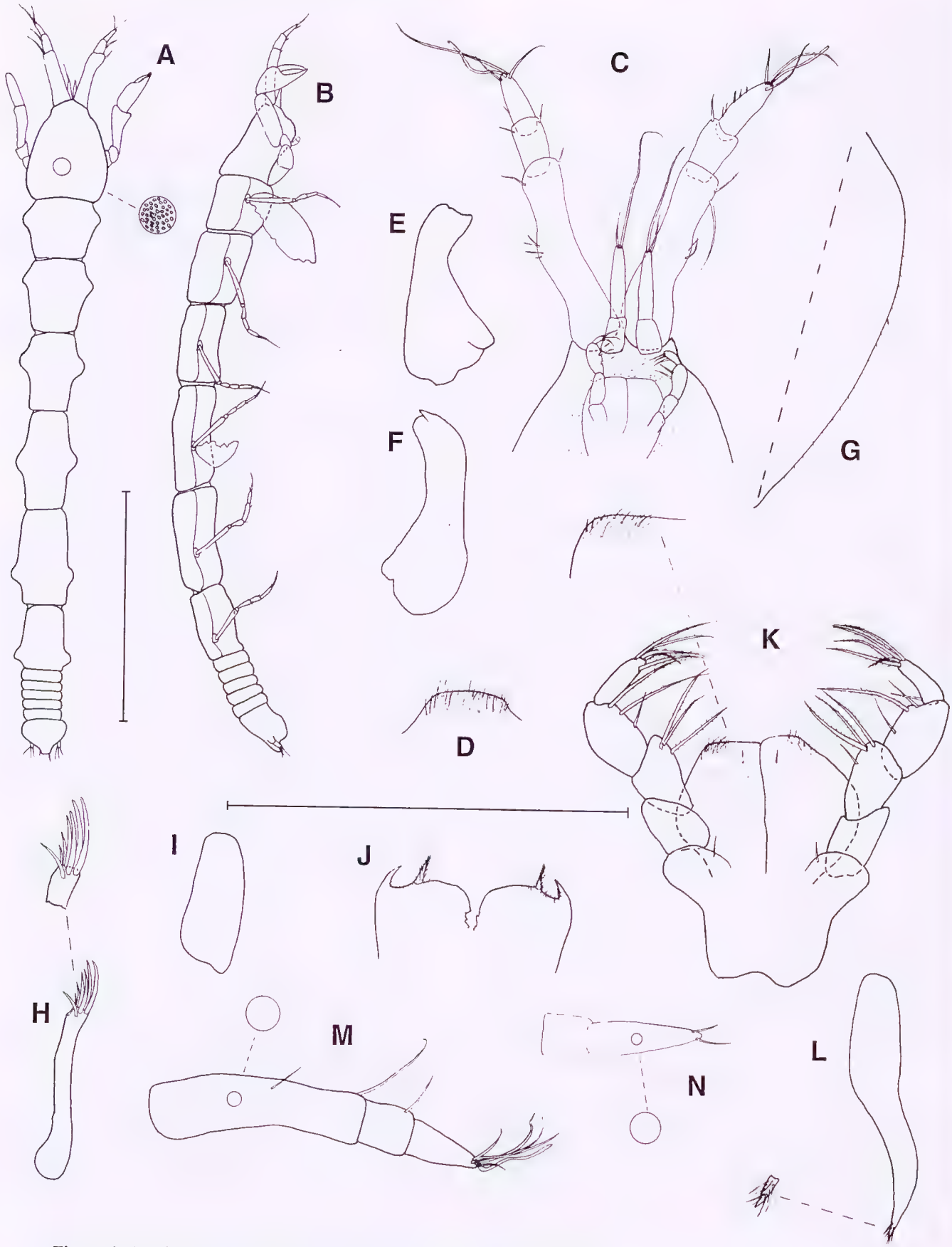

Figure 1. *Agathotanais manganicus* n.sp., A–C, ♀ holotype, AM P51003—A, dorsal view; B, lateral view; C, ventral view of anterior carapace; scale bar for A and B = 1 mm. *Agathotanais manganicus* n.sp. D–N, ♀ paratype, AM P50999—D, labrum; E, left mandible; F, right mandible; G, anterior margin of first oostegite; H, maxillule, palp not shown; I, maxilla; J, labium; K, maxilliped; L, epignath; M, antennule; N, antenna; scale bar for mouthparts = 0.25 mm.

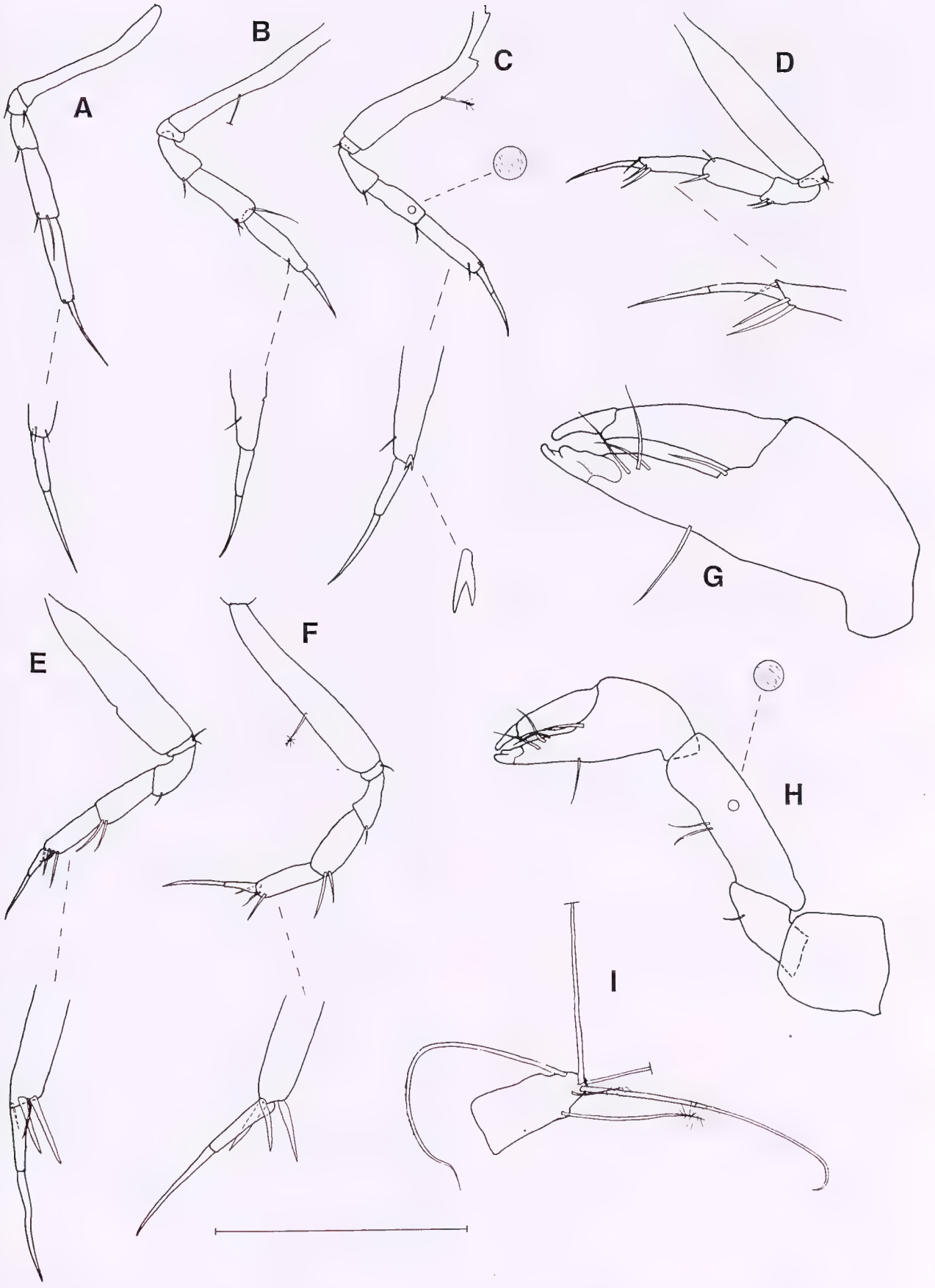

Figure 2. *Agathotanais manganicus* n.sp., ♀ paratype AM P50999—A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, cheliped; H, cheliped propodus and dactylus; I, uropod; scale bar = 0.3 mm.

2 distal simple setae on tergal margin and 1 sternally; *propodus* with 1 short simple seta on tergal margin. *Pereopod 3* (Fig. 2C) similar to pereopod 1 except *basis* with 1 plumose seta near midlength on sternal margin; *ischium* with 1 seta only; *carpus* with 1 distal seta on tergal margin; *propodus* with 1 short simple seta on tergal margin, and a denticulate scale on sternal margin. *Pereopod 4* (Fig. 2D) similar to pereopod 1 except *basis* somewhat wider; *merus* with 2 distal simple stout setae on tergal margin; *carpus* with 1 distal simple stout seta on tergal margin and 1 simple short seta on sternal margin; *propodus* with 2 distal simple stout setae on tergal margin and 1 simple short seta on sternal margin. *Pereopod 5* (Fig. 2E) similar to pereopod 4 except *merus* with 1 distal simple seta on tergal margin; *carpus* with 2 distal simple stout setae on tergal margin. *Pereopod 6* (Fig. 2F) similar to pereopod 4 except *basis* with 1 plumose seta midlength on sternal margin; *ischium* with 1 simple seta only; *merus* with 1 distal simple seta on tergal margin; *carpus* with 2 distal simple stout setae on tergal margin; *propodus* with 3 distal simple stout setae on tergal margin. *Pleopods* absent in females. *Uropods* (Fig. 2I) uniramous. *Endopod* uniarticulate, with 3 long, 1 short simple and 1 short plumose seta distally, exopodal process with 1 long distal plumose long.

Remarks. The unique two articulated antenna of *Agathotanais manganicus* n.sp. is considered the most pleisiomorphic condition within *Agathotanais* and made it necessary to modify the generic diagnosis.

Agathotanais ahyongi n.sp.

Material examined. HOLOTYPE (AM): 1 nonovigerous ♀ (body length 3.7 mm), DOMES site A station DJ69, AM P51007. PARATYPES: 1 nonovigerous ♀, mouthparts and limbs dissected; 1 ♂, 1 juvenile ♀, 2 mancas, DOMES site A station DJ73, AM P51009. 1 nonovigerous ♀, DOMES site A station DJ38, cut in two, mounted on SEM stub and coated, AM P51002. 1 ♂, DOMES site A station DJ 77, AM P51013.

Diagnosis. Antennule article 1 no longer than rest of antennule. Antenna reduced into lobes not visible in the compound scope. *Labium* without median plumose seta. Pereonite 6 longer than broad (l/w ratio 1.4).

Etymology. Named after my friend and fellow student Shane T. Ahyong.

Description of adult female (Fig. 3A,B). *Body* cylindrical, slender. *Cephalothorax* (Fig. 3O) shorter than first 2 pereonites; anterolateral corners convex. *Pereonites*. Pereopod shoulders placed anteriorly on pereonite 1, near midlength on pereonites 2–4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long l/w ratio 0.9, shorter than other pereonites. *Pereonite 2–6* l/w ratio 1.3, 1.4, 1.6, 1.7, 1.4 respectively. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* longer than last 3 pleonites together, rounded in lateral view, apex margin straight. *Antennule* (Fig. 3E) with 3 articles. *Article 1* as long as rest of antennule, with 1 simple seta midlength and 3 distally. *Article 2* less than 0.5 times of article 3 length, smooth. *Article 3* with 4 long setae distally. *Antenna* (Fig. 3N). Minute lobe-like structures without setae. *Mouthparts*. *Labrum* (Fig. 3G), distal margin with small medial lobe, setose. *Labium* (Fig. 3L) with anterolateral processes but without plumose seta midlength. *Mandibles* molar process consists of membranous lobe only. *Left mandible* (Fig. 3H) 0.3 times larger than right mandible; incisor with 3 denticles; lacina consisting of 1 small lobe and a minute accessory lobe. *Right mandible* (Fig. 3I) incisor with 3 denticles. *Maxillule* (Fig. 3J) endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 3K) elongate without recognisable features. *Maxilliped* (Fig. 3M) basis fused medially. Endite elongate, not fused medially and more heavily setose on anterolateral corners. Palp article 1 quadrate, smooth; article 2 rectangular, with 1 distal seta; article 3 with 2 setae on inner margin; article 4 with 4 distal setae. *Epignath* not found. *Cheliped* (Fig. 4A). *Basis* rectangular, less than half length of carpus. *Merus* smooth, ovoid. *Carpus*, about as long as propodus, smooth. *Propodus* (Fig. 4B) tergal surface irregular at widest point, with 1 simple seta midlength on sternal margin. *Fixed finger* with 1 distal seta on each margin and blunt process by insertion of distal tooth. *Dactylus* with 2 small spiniform setae on inner margin but without bifurcate process at distal tooth insertion. *Oostegites*. No ovigerous specimens found. *Pereopod 1* (Fig. 4C). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* smooth. *Merus* expanding in width distally, shorter than carpus, smooth. *Carpus* longer than dactylus and terminal spine together, with 1 distal simple seta. *Propodus* as long as carpus, with row of small tergal setae. *Dactylus* and terminal spine 0.5 propodus. *Pereopod 2* (Fig. 4D) similar to pereopod 1 except *ischium* with 1 sternal seta; *merus* with 1 sternal seta; *carpus* with 2 short sternal setae. *Pereopod 3* (Fig. 4E) resembles pereopod 2 except *carpus* with 2 longer sternal setae. *Pereopod 4* (Fig. 4F). *Basis* somewhat wider than 3 preceding pereopods, smooth. *Ischium* with 1 simple seta. *Merus* expanding in width distally, with 1 distal simple seta on tergal margin. *Carpus* longer than propodus, with 2 distal simple stout seta. *Propodus* with 3 distal simple stout setae. *Dactylus* and terminal spine marginally shorter than propodus. *Pereopod 5* (Fig. 4G) resembles pereopod 4 except *basis* tergal margin with 2 plumose setae; *merus* with 2 distal tergal setae; *carpus* with 3 distal stout simple setae; *propodus* with 3 distal simple stout setae and row of evenly spaced small simple setae on tergal margin; *dactylus* lost. *Pereopod 6* (Fig. 4H) similar to pereopod 4 except *basis* with 1 plumose seta; *ischium* smooth; *merus* with 2 setae; *carpus* with 3 distal simple stout setae; *propodus* with 3 distal stout setae and row of small setae; *dactylus* and terminal spine longer than propodus. *Pleopods* absent in females. *Uropods* (Fig. 3N) uniramous, uniarticulate and with 2 short and 2 distal long simple setae.

Description of male (Fig. 3C,D). *Pereon*. Pereonite 1 longer and narrower than female, shoulders less prominent. *Pleotelson* only marginally wider than pleon. *Pleopods* (Fig. 3F). All 5 pairs similar. *Exopod* and *endopod* armed with 8 simple setae on rami.

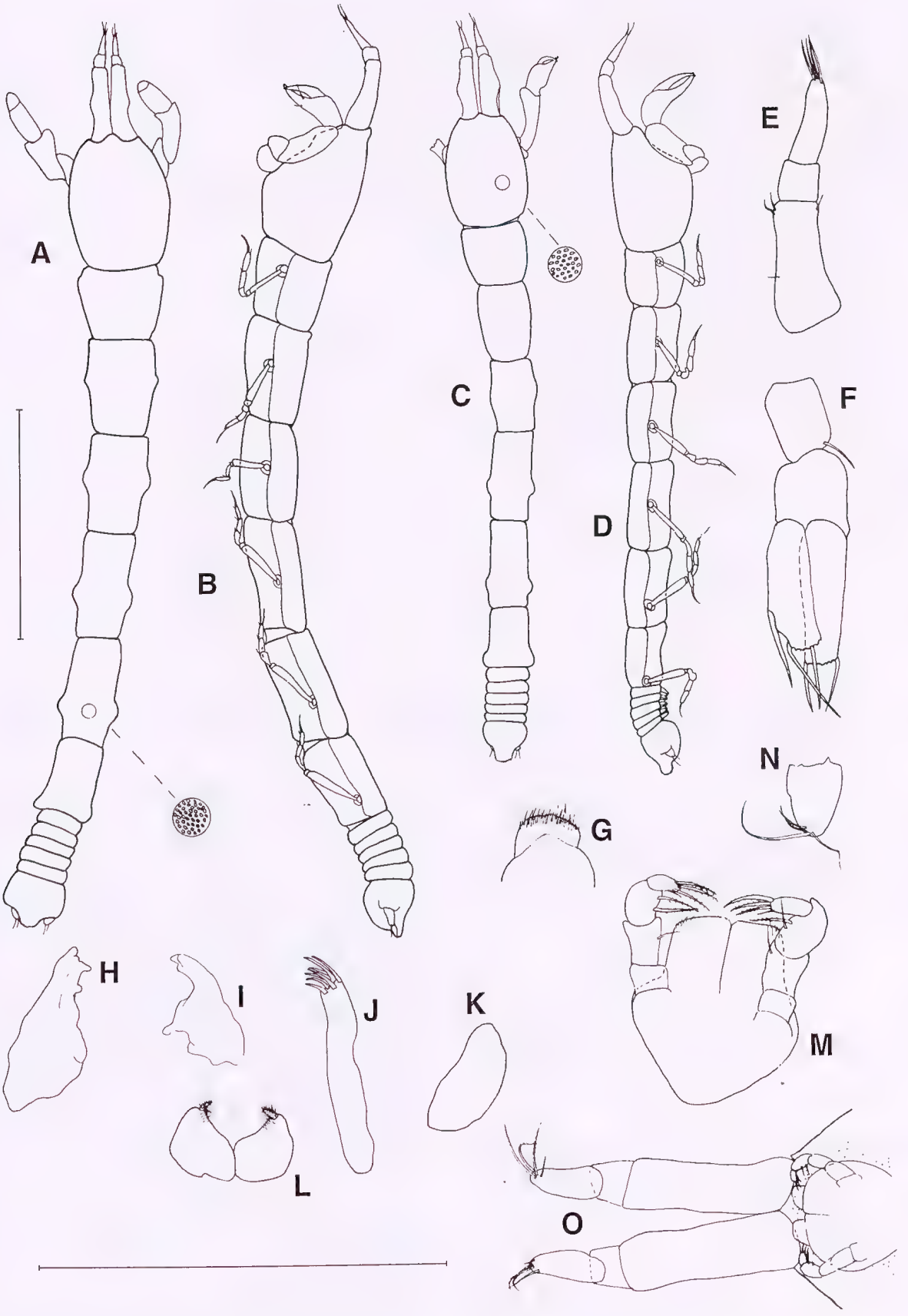

Figure 3. *Agathotanais ahyongi* n.sp., A, B & O, ♀ holotype AM P51007—A, dorsal view, scale bar = 1.0 mm; B, lateral view; O, cephalothorax, ventral view. *Agathotanais ahyongi* n.sp., C, D & F, juvenile ♂ paratype AM P51009—C, dorsal view; D, same lateral view; F, pleopod. *Agathotanais ahyongi* n.sp., E, G–N, ♀ paratype AM P51009—E, antennule; G, labrum; H, left mandible; I, right mandible; J, maxillule, palp not shown; K, maxilla; L, labium; M, maxilliped; N, uropod; scale bar for mouthparts = 0.25 mm.

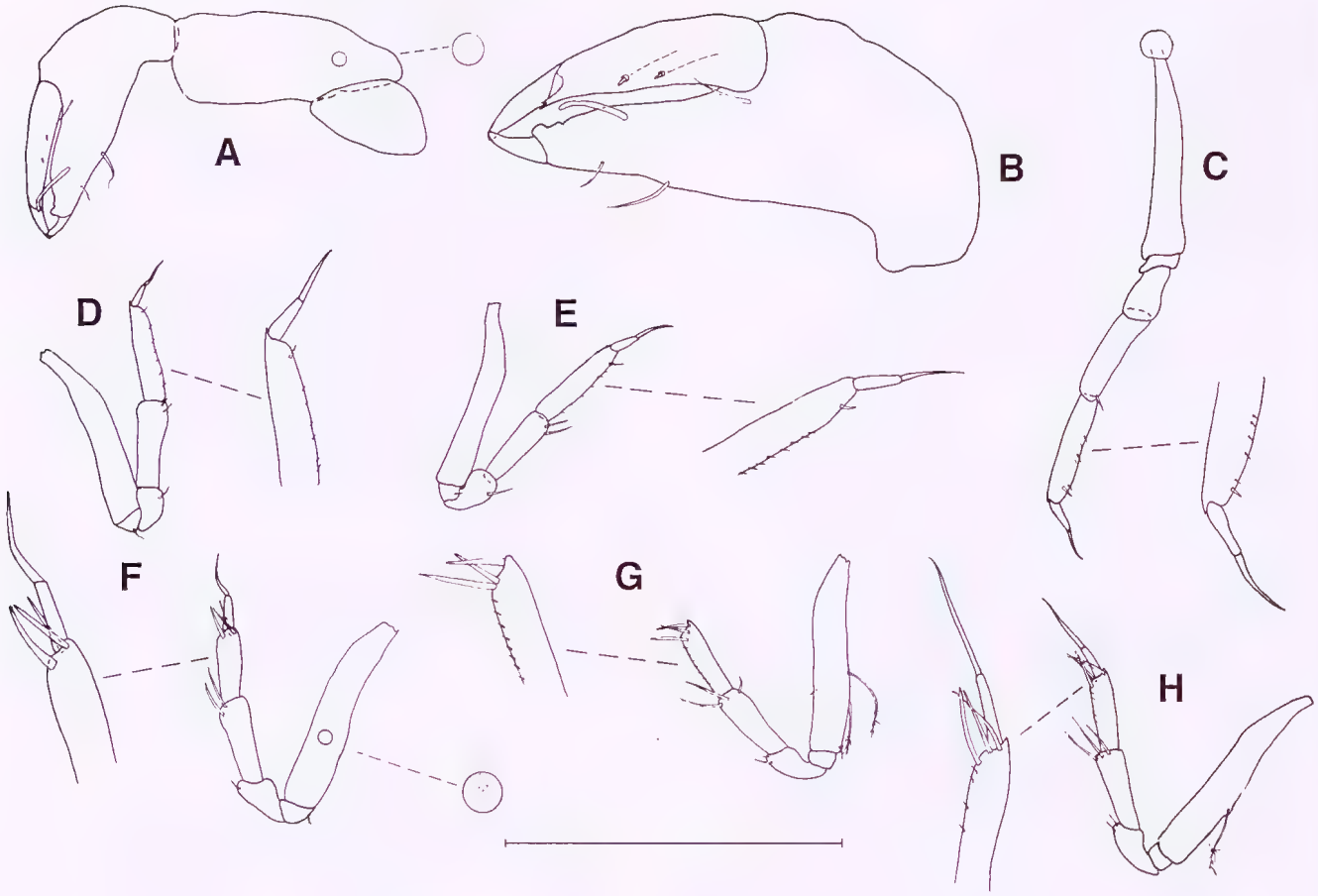

Figure 4. *Agathotanais ahyongi* n.sp., ♀ paratype AM P51009—A, cheliped; B, cheliped propodus and dactylus; C, pereopod 1; D, pereopod 2; E, pereopod 3; F, pereopod 4; G, pereopod 5; H, pereopod 6; scale bar = 0.3 mm.

Remarks. The reduction of the antenna to a lobe-like process reflects highest degree of reduction of this appendage within the Tanaidacea. The mouthparts of this species are significantly smaller than in other *Agathotanais* species.

Agathotanais spinipoda n.sp.

Material examined. HOLOTYPE (MV): 1 nonovigerous ♀ (body length 3.6 mm), slope station 69, MV J37856. PARATYPES (MV): 1 nonovigerous ♀, mouthparts and limbs dissected, slope station 27, MV J37880; 1 nonovigerous ♀, slope station 27, cut in two, mounted on SEM stub and coated, MV J37880.

Other material (MV). 26 nonovigerous ♀♀, 2 ♂♂, 11 juvenile ♀♀, 3 juvenile ♂♂, slope station 69; 1 nonovigerous ♀, 2 ♂♂, 1 manca II, slope station 32; 1 nonovigerous ♀, slope station 53; 1 ♂, slope station 33; 2 nonovigerous ♀♀, slope station 67; 10 nonovigerous ♀♀, 2 ♂♂, slope station 27; 8 nonovigerous ♀♀, 1 ♂, slope station 40.

Diagnosis. Antennule article 1 longer than rest of antennule. Antenna less than 0.3 times of antennule article 1 length. Pereopod 4–6 propodus with row of small spines. Pereonite 6 wider than long (l/w ratio 0.9). Uropods not extending beyond pleotelson apex.

Etymology. Name refers to the unusual spines on the propodus and carpus of pereopods 4–6.

Description of adult female (Fig. 5A,B). *Body* cylindrical, stout. *Cephalothorax* (Fig. 5G) shorter than first 2 pereonites, anterolateral corners slightly concave. *Pereonites*. Pereopod shoulders are placed anteriorly on pereonite 1, midlength on pereonites 2–4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long, l/w ratio 0.6, shorter than other pereonites. *Pereonite 2–6* l/w ratio 0.7, 0.85, 0.95, 1.05, 0.9. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* as long as last 2 pleonites together, apex margin straight. *Antennule* (Fig. 5E) with 3 articles. *Article 1* twice as long as rest of antennule, with 2 simple setae midlength and 4 distally. *Article 2* 0.5 times article 3 length, with 1 distal thick seta. *Article 3* with at least 2 distal long setae. *Antenna* (Fig. 5F) uniarticulate, less than 0.3 times antennule article 1, with row of small setae. *Mouthparts*. *Labrum* (Fig. 6A), distal margin with small medial lobe, setose. *Left mandible* (Fig. 6B) incisor bifurcate, lacina consists of tiny lobe only. *Right mandible* (Fig. 6C) incisor consists of 1 blunt tooth. *Labium* (Fig. 6D) with anterolateral processes and plumose spiniform seta midlength. *Mandibles* molar process consisting of membranous lobe only. *Maxillule* (Fig. 6E)

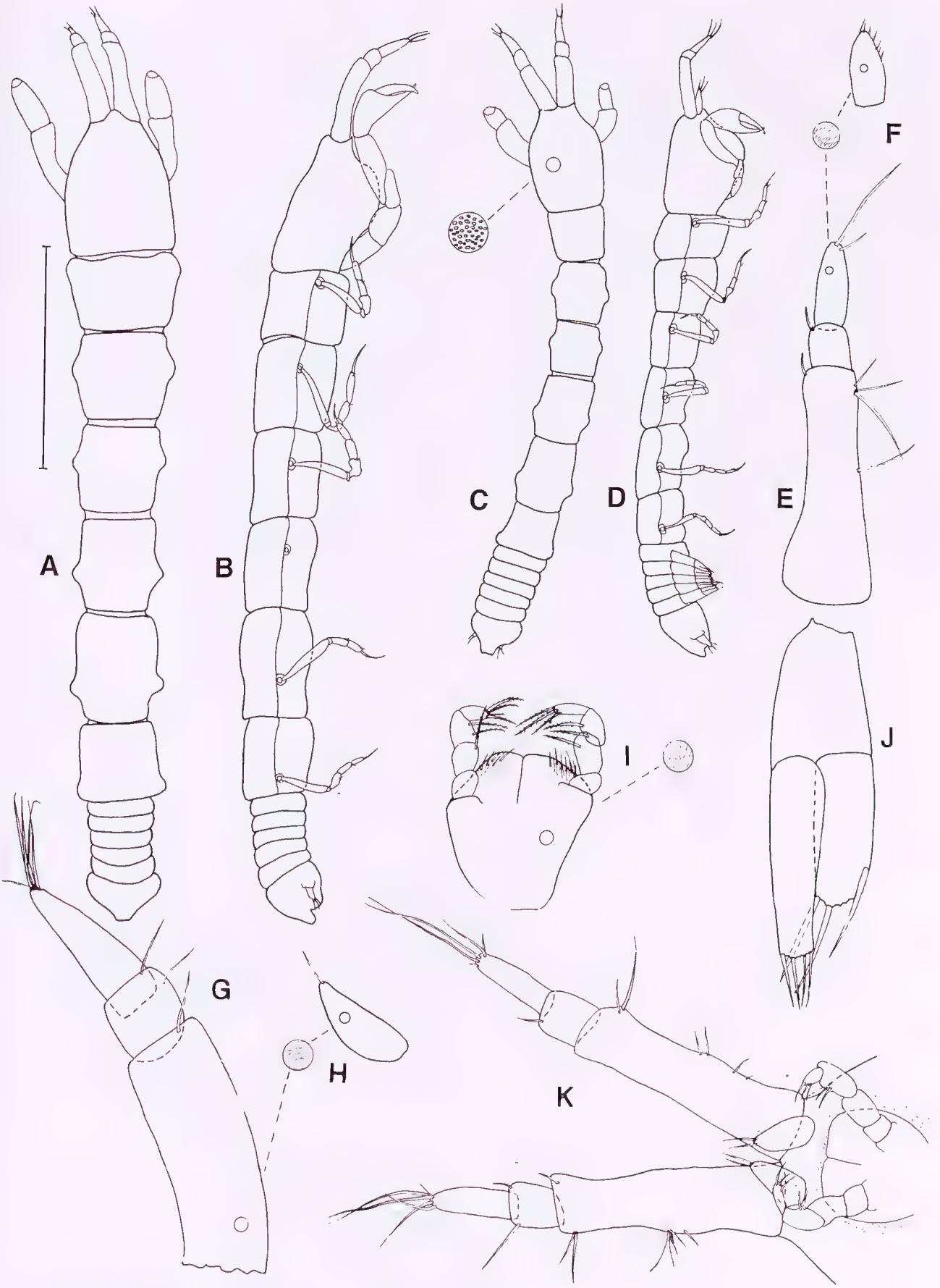

Figure 5. *Agathotanais spinipoda* n.sp., A, B & K, ♀ holotype MV J37856; C, D, G–J, ♂ paratypes, and E, F, ♀ paratype, MV J37880. A, ♀ dorsal view, scale bar = 1.0 mm. B, same lateral view; C, ♂ dorsal view; D, same lateral view; E, ♀ antennule; F, ♀ antenna; G, ♂ antennule; H, ♂ antenna; I, ♂ maxilliped; J, pleopod; K, cephalothorax, ventral view.

endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 6F) extremely elongate with no discernible features. *Maxilliped* (Fig. 6G) basis fused medially. Endites with proximal lobes and more heavily setose on anterolateral corners. Palp article 1 outer margin longer than inner, smooth; article 2 inner margin longer than outer and with 3 distal setae; article 3 with 3 setae on inner margin; article 4 with 4 distal setae. *Epignath* (Fig. 6H) with distal setules. *Cheliped* (Fig. 7G). *Basis* rectangular, less than half the length of carpus. *Merus* with 1 simple seta sternally. *Carpus* subequal to propodus, with 1 simple seta midlength and 1 distally on each margin. *Propodus* (Fig. 7H) tergal surface uneven at widest point, with 1 simple seta midlength on sternal margin and 1 by dactylus insertion. *Fixed finger* with 2 distal setae on inner margin and pointed process by insertion of distal tooth. *Dactylus* with bifurcate process next to insertion of distal tooth and 2 small spiniform setae on inner margin. *Oostegites*. No ovigerous specimens found. *Pereopod 1* (Fig. 7A). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* with 1 distal simple seta on tergal margin. *Merus* expanding in width distally, shorter than carpus, with 2 distal simple setae on tergal margin. *Carpus* shorter than dactylus and terminal spine together, with 1 distal simple seta on each margin. *Propodus* 0.3 times longer than carpus, with 1 distal simple seta and denticulate scale. *Dactylus* and terminal spine as long as propodus. *Pereopod 2* (Fig. 7B) similar to pereopod 1 except *merus* smooth, *propodus* with 1 distal short spine on sternal margin. *Pereopod 3* (Fig. 7C) similar to pereopod 1 except *carpus* with 2 distal setae on tergal and 1 on sternal margin. *Pereopod 4* (Fig. 7D). *Basis* somewhat wider than on other pereopods; tergal margin with 2 plumose setae sternally with 1 simple seta. *Ischium* band shaped with 2 distal simple setae. *Merus* expanding in width distally, with 2 distal simple setae on tergal margin. *Carpus* as long as propodus, with 1 simple stout seta distally and 3 short spines on tergal margin. *Propodus* with 3 distal simple stout setae and 5 short spines on tergal margin. *Dactylus* and terminal spine longer than propodus and weakly setulate. *Pereopod 5* (Fig. 7E) similar to pereopod 4 except *basis* tergal margin with 2 plumose setae, *propodus* with 3 tergal spines, *dactylus* and terminal spine appear smooth. *Pereopod 6* (Fig. 7F) similar to pereopod 4 except *basis* without plumose setae, *merus* with 1 seta only, *carpus* with 1 distal simple stout seta and 2 short spines on tergal margin, *propodus* with 3 distal stout setae and 3 short spines on tergal margin, *dactylus* and terminal spine appear smooth. *Pleopods* absent in females. *Uropods* (Fig. 7I) uniramous, uniarticulate and with 3 long and 1 short simple and 1 distal plumose seta and 1 simple and plumose setae at point of narrowing. Long simple seta on exopod process.

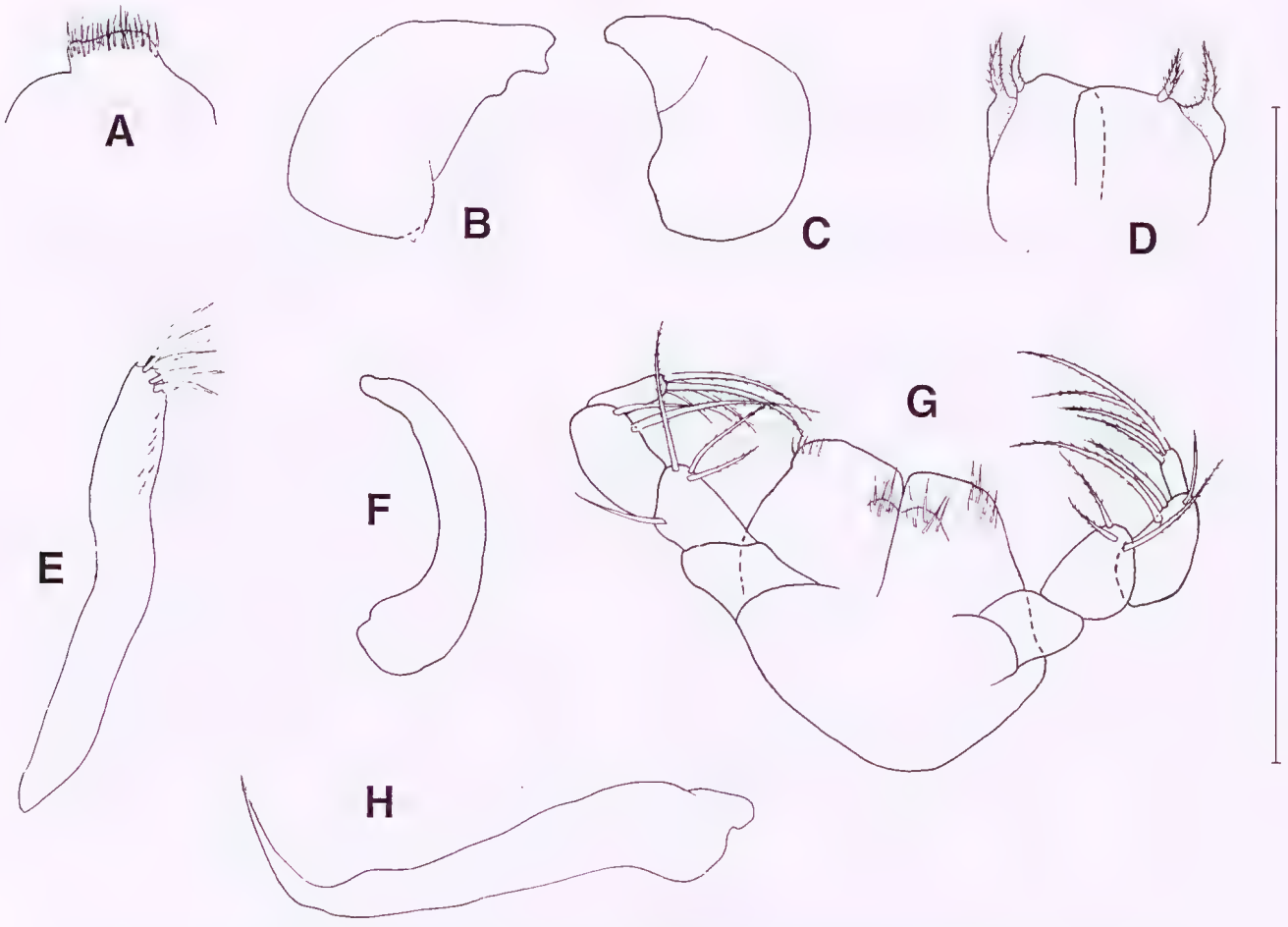

Figure 6. *Agathotanais spinipoda* n.sp., ♀ paratype MV J37880—A, labrum; B, left mandible; C, right mandible; D, labium; E, maxillule, palp not shown; F, maxilla; G, maxilliped; H, epignath; scale bar = 0.25 mm.

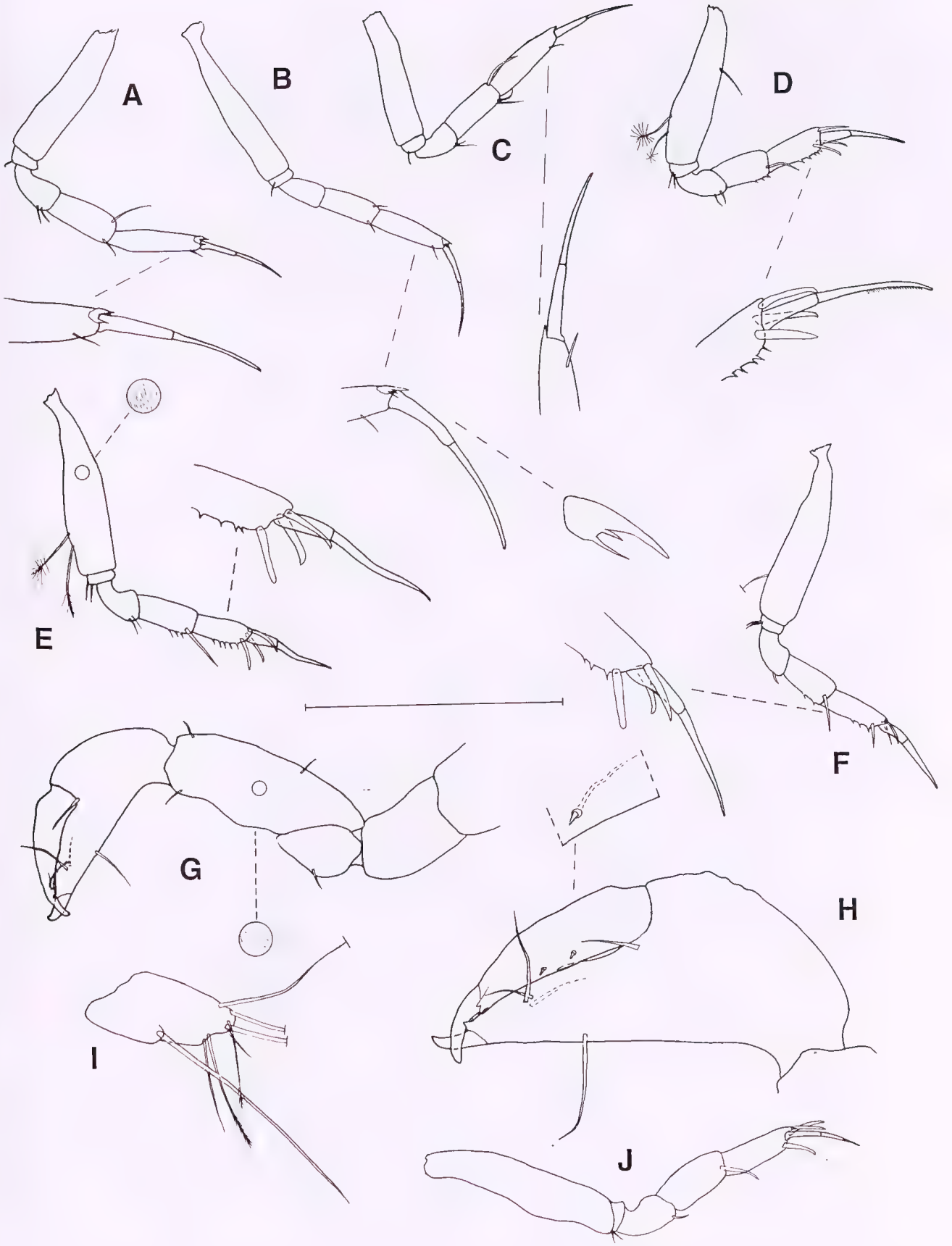

Figure 7. *Agathotanais spinipoda* n.sp., A–I, ♀ paratype MV J37880. A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, cheliped; H, cheliped propodus and dactylus; I, uropod; J, ♂ pereopod 5; scale bar = 0.3 mm.

Description of male (Fig. 5C,D). *Pereon*. Pereopod 1 longer and narrower than that of female, shoulders less prominent. *Pleotelson* not wider than pleon. *Maxilliped* (Fig. 5I) smaller than female and endites without proximal lobes. *Antennule* (Fig. 5G) thicker and longer than in female (more than 0.25 times), with distal aesthetasc. *Antenna* (Fig. 5H) 0.5 times longer than female antenna. *Pereopods* (Fig. 7J) without propodus spines. *Pleopods* (Fig. 5J). All 5 pairs similar, *exopod* armed with 8 and *endopod* with 7 simple setae on rami.

Remarks. A common species on the southeast Australian slope at bathyal depths (400–1840 m). The tubes made of mud sediment particles and a few sponge spicules. *Agathotanais spinipoda* n.sp. shares the pereopod 4–6 spine character with *A. ghilarovi* but can be distinguished from it by the lack of maxilliped endite denticles, by the broad antennule and longer antennule article 1.

Agathotanais sp. incertae sedis

Material examined. 1 nonovigerous ♀, DOMES site A station DJ41; 1 manca, DOMES station DJ15. Additional material originally identified as *Agathotanais hanseni*, are possibly also this species but the poor condition of the specimens does not allow confirmation; 2 nonovigerous ♀♀, 1 fragment, USAP station 3, "Chilii Trench", 16°12'S 74°41'W, 2599–5858 m; 2 nonovigerous ♀♀, USAP station 12, Taomin Sea, 40°00.42'S 153°00.03'W, 4564 m.

This species is not described because only one adult specimen is available. It is, however, easily distinguished from the other species of *Agathotanais* by the pleotelson apex being sharply pointed.

Key to species of the genus *Agathotanais*

1 Antenna absent ..... *A. ahyongi* n.sp.

—— Antenna present 2

2 Antenna consisting of 2 articles ..... *A. manganicus* n.sp.

—— Antenna uniarticulate 3

3 Pereopod 4 propodus with tergal row of small spines 7

—— Pereopod 4 propodus without tergal row of small spines 4

4 Pereonites 4 + 5 wider than long. Carapace as long as pereonites 1 + 2 together ..... *A. brevis**

—— Pereonites 4 + 5 longer than wide or subequal. Carapace shorter than pereonites 1 + 2 together 5

5 Pereonites 4 + 5 subequal in length and width ..... *A. ingolfi*

—— Pereonites 4 + 5 longer than wide 6

6 Pleon narrower than pereon ..... *A. hanseni*

—— Pleon as wide as pereon ..... *A. splendius**

7 Antennule article 1 almost 3 times longer than article 3. Maxilliped endites without caudodistal denticles ..... *A. spinipoda* n.sp.

—— Antennule article 1 only 1.5 times longer than article 3. Maxilliped endites with caudodistal denticles ..... *A. ghilarovi**

* Specimens of *Agathotanais splendius*, *A. ghilarovi* and *A. brevis* could not be obtained and key characters are taken from the original descriptions only.

Discussion

Sieg (1983) stated that *Agathotanais* is defined by apomorphic characters but without direct references to which. Sieg (1983) did, however, claim that most reductions within the Tanaidacea are apomorphic character trends. If this is true, then the apomorphic characters are: 3-articulated antennule, rudimentary antenna, reduction of adult male mouthparts and absence of uropodal exopod. A preliminary phylogenetic analysis using the Apseudomorpha, Neotanaidomorpha and *Tanais* as outgroups, supports this view and suggests that the other diagnostic features (i.e. ventral cheliped attachments, heavily calcified cuticle, labial processes, modified male pleopods) are also apomorphic trends, while the limited sexual dimorphism is a pleisiomorphic character (Larsen, research in progress).

Within *Agathotanais* the above mentioned reductions vary considerably. The long, 2-articulated antenna of *A. manganicus* n.sp. may represent a plesiomorphic character state, approaching that of the *Paragathotanais* and *Paranarthrura*. The reduction of the antenna to a lobe-like structure in *A. ahyongi* n.sp. may represent an apomorphic trend. *Agathotanais ahyongi* also displays a loss of median plumose seta on the labium, otherwise thought to be an apomorphic generic character. The reduction of male mouthparts have long been considered an apomorphic trend (Sieg, 1986). This reduction is closely coupled to sexual maturity (Lang, 1953). As seen in *A. spinipoda* n.sp., juvenile male *A. spinipoda* (defined by the incompletely developed pleopods) did have a complete set of mouthparts, resembling, but not identical to, those of the adult female. Males with completely developed pleopods retain only a small maxilliped and the epignath.

Agathotanais as currently defined, is a cosmopolitan genus, found in the northeast- and northwest Atlantic, southeast Atlantic, Central American Pacific slope, mid- and northeast Pacific, the eastern slope of Australia and in the Indian Ocean. This distribution pattern is similar to that of most tanaid genera. So far, extensive new Pacific/Australian material has revealed only one genus (*Bathytanais*), which appears to have a distribution restricted to the Australian region. Tanaids may thus follow the distribution patterns of amphipods and cumaceans in the deep sea and not those of isopods (Hessler & Wilson, 1983).

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A New Genus and Two New Species of Myrophine Worm-eels, with Comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae)

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ABSTRACT. *Skythrenchelys* n.gen. differs from other myrophine ophichthids in the condition of its gill openings (moderately elongate and below lateral midline), dentition (large, conical and uniserial), posterior nostril (entirely outside mouth), and other characters. *Skythrenchelys zabra* n.sp., the type species, is described from India, the Philippines, Indonesia and northern Australia; *S. lentiginosa* n.sp. is described from the Red Sea. *Scolecenchelys* Ogilby, previously a subgenus of *Muraenichthys* Bleeker, is generically distinct on the basis of differences in dentition (teeth conical and uniserial or biserial *vs* blunt and multiserial), cephalic pores (2 pores between anterior and posterior nostrils *vs* 1 pore), and its posterior nostril condition (within *vs* outside mouth). Valid species of *Muraenichthys* and *Scolecenchelys* and their synonyms are identified.

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The most recent revision of the snake-eel and worm-eel family Ophichthidae (McCosker *et al.*, 1989) recognised 55 genera, including 44 in the Subfamily Ophichthinae and 11 in the Myrophinae. The family is worldwide in distribution, principally but not exclusively in inshore waters of tropical seas. Its members mainly live burrowed tail first in soft sediments and readily avoid capture by most sampling methods, though they are variously vulnerable to ichthyocides. This may explain why some of the approximately 250 ophichthid species are known from few or even single specimens. Ophichthids have distinctive leptocephali, many of which were documented in the Atlantic by Leiby (1989), though most have not yet been identified.

The comprehensive treatment of the Ophichthidae by McCosker *et al.* (1989) brought together what is known of the western North Atlantic species in this family. In contrast, the ophichthid fauna of the Indo-west Pacific is much less well known. Localities where soft sediments of coral sand to mud predominate occur widely but are poorly sampled and warrant further attention. It is expected that new ophichthid taxa will be found from time to time in the Indo-west Pacific, as evidenced by recent records and by those reported here. This paper describes a new genus and two new species of myrophine worm-eels from such habitats, and reviews the related genera *Muraenichthys* Bleeker, 1853 and *Scolecenchelys* Ogilby, 1897.

The worm-eels of the subfamily Myrophinae comprise approximately 55 species distributed among 11 genera. The majority have been uncomfortably assigned to the genera *Myrophis* Lütken, 1851 (seven to eight species), *Pseudomyrophis* Wade, 1946 (eight species), and *Muraenichthys* (about 25 species) in that they lack characters so outstanding as to allow recognition of monophyletic lineages. In his treatment of the osteology and relationships of the Ophichthidae, McCosker (1977) identified subgeneric lineages within *Muraenichthys* but was hesitant to recognise them at the generic level pending a more thorough analysis of the species within that complex assemblage.

Several years ago we were provided with specimens of two remarkable new species, described herein, whose affinities were clearly with *Muraenichthys* (sensu lato). However, we were reluctant to describe them within that genus because of their unique physiognomy and associated characters. After the examination of specimens of most of the Tribe Myrophini, we are now confident in describing them as species of a new genus and at the same time separating two lineages within *Muraenichthys*. In particular, we herein elevate the subgenus *Scolecenchelys* to generic rank. This work is not meant to be a revisionary study of either genus in that numerous problems remain concerning the limits of species which we therefore conservatively retain.

Methods

Measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length, body length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; maximum body depth does not include the median fins. Head pore terminology follows that of McCosker *et al.* (1989) such that the supraorbital pores (SO) are expressed as the ethmoid pore + pores in supraorbital canal, e.g., 1 + 3; infraorbital pores (IO) are expressed as pores along the upper jaw + those in vertical part of canal behind eye (the "postorbital pores"), e.g., 4 + 1, in that the last pore included along the upper jaw is part of the postorbital series; the preoperculomandibular pores (POM) include those along the lower jaw and those on the preopercular canal; the supratemporal pores (ST) include those on the dorsolateral side of the head in front of the lateral line pores. The median frontal and supratemporal pores are not included since they are present in all specimens examined. We are not fully satisfied that the numbers of POM pores and our interpretation of them that we have given is definitive. For example, the 6th mandibular pore may well be the first of the preopercular series, such is the extent of posterior displacement of the jaw angle; also, the stained paratype of *S. zabra* n.sp. (CAS 99802) shows just 2 pores in the preopercular series, confirmed in the unstained CAS specimen, while the NMNZ holotype and 2 paratypes apparently have 3 preopercular pores. Osteological examination involved clearing and counterstaining with alcian blue and alizarin red dyes (Dingerkus & Uhler, 1977). Vertebral counts (which include the hypural) were taken from radiographs. Radiographic techniques are described in Böhlke (1989). The mean vertebral formula (MVF) is expressed as the average of predorsal, preanal, and total vertebrae (Böhlke, 1982). Institutional abbreviations used in the text and figures are as listed in Leviton *et al.* (1985). All material is deposited in one or other of the above institutions, as indicated in the text.

AMS	Australian Museum, Sydney
BPBM	Bernice P. Bishop Museum, Honolulu
CAS	California Academy of Sciences, San Francisco
MNHN	Muséum national d'Histoire naturelle, Paris
NMNZ	National Museum of New Zealand, Wellington
NTM	Northern Territory Museum, Darwin
SIO	Scripps Institution of Oceanography, La Jolla, USA
USNM	United States National Museum, Washington D.C.

Skythrenchelys n.gen.

Type species. *Skythrenchelys zabra* n.sp.

Material examined. Holotypes and paratypes of *S. zabra* n.sp. and *S. lentiginosa* n.sp. Cleared and stained material: paratype of *S. zabra* n.sp., CAS 99802, TL 282 mm; *Muraenichthys gymnopterus* (Bleeker, 1853), CAS 61117, TL 184 mm; CAS 98928, TL 242 mm; SIO 69-276, TL 144 mm; *M. schultzei* Bleeker, 1857, CAS 35587, TL 176 mm; paratype of *Scolecenchelys chilensis* (McCosker, 1970), SIO 65-645, TL 248 mm; *S. gymnotus* (Bleeker, 1857), CAS 64946, TL 249 mm; SIO 69-266, TL 244 mm; *S. macropterus* (Bleeker, 1857), SIO 69-277, TL 181 mm.

Diagnosis. Elongate myrophines, Tribe Myrophini (*sensu* McCosker, 1977), with tail equal to or shorter than head and trunk, laterally compressed posteriorly. Snout conical, its underside not grooved and extending just beyond tip of lower jaw. Anterior nostril in a short tube that does not extend beyond lip; posterior nostril a hole with a small anterior flap, entirely above margin of upper lip, slightly below and in advance of orbit. Jaws elongate, centre of orbit in advance of middle of upper jaw. Lips smooth, without crenulae or barbels. Gill opening below lateral midline, unconstricted and elongate for a myrophine, nearly equal in length to isthmus. Median fins low but apparent; dorsal fin origin along trunk or above anus. Pectoral fins absent or a minute remnant. Cephalic and lateral line pores

developed; supraorbital, frontal, infraorbital, preoperculo-mandibular and supratemporal pore (including median supratemporal) series present; lateral line pores absent from posterior third of tail. Teeth conical and large, uniserial on jaws and vomer. Gill arches not well developed; upper pharyngeal tooth plates closely sutured but not fused. Neurocranium stout, sub-truncate posteriorly, supraoccipital crest barely developed. Jaws elongate, suspensorium posteriorly inclined, about 60° to horizontal; maxillae elongate and tapering posteriorly. Opercle and preopercle developed, other elements cartilaginous or absent. Branchiostegal rays typically myrophine (*sensu* McCosker, 1977), 6 attached to outer face of each epihyal with 32 unattached pairs well behind the basal arch. Pectoral girdle reduced to stout cleithrum and thin supracleithrum. Epipleural ribs on all precaudal vertebrae. Other characters those of the two species.

Distribution. Known from two species, ranging from the Red Sea and the Indian and western Pacific oceans, respectively.

Etymology. From Greek *skythros* (angry or sullen) and *enchelys* (an eel), in reference to the facial expression of the two included species. Treated as feminine according to Opinion 95 of the *Bulletin of Zoological Nomenclature*, 1970.

Affinities of the genus. The species of *Skythrenchelys* n.gen. are unique within the Myrophini in the conditions of their gill opening size and location, their dentition, and the inclination of the suspensorium and associated elongation of the jaws. They share with species of *Muraenichthys* the condition of their posterior nostril and the presence of but one supraorbital pore between the anterior and posterior nostrils. As well, *Skythrenchelys* n.gen. and *Muraenichthys* are more similar to each other in certain osteological characters (note: this analysis is based on the osteological preparation of *S. zabra* n.sp.; the single, small specimen of *S. lentiginosa* n.sp. only allowed radiographic examination) such as the slender supracleithrum, stout cleithrum, and the general shape of the neurocranium, than to those of other myrophines. The species of *Skythrenchelys* further differ from all other myrophines in the characters listed in the Key and in Table 1.

Upon cursory examination, the species of *Skythrenchelys* n.gen. are obviously myrophine in appearance, and could be mistaken for certain species of *Scolecenchelys*. The condition of the elongate jaw and the enlarged dentition are unique, and will differentiate them from any other myrophine.

Table 1. Characteristics of the genera *Skythrenchelys* n.gen., *Muraenichthys* and *Scolecenchelys*. IOP = infraorbital pore between anterior and posterior nostrils; POP^3 = third preopercular pore.

character	*Skythrenchelys* n.gen.	*Muraenichthys*	*Scolecenchelys*
gill opening	unconstricted	constricted	constricted
centre of orbit	before mid-jaw	≈ mid-jaw	behind mid-jaw
dentition	conical, mostly uniserial	blunt, multiserial	conical, uniserial or biserial
posterior nostril	in outer lip, with a small flap	in outer lip, with a prominent flap	inside of or along lip
POP^3	present or absent	present or absent	present
IOP	1	1	2

Key to the genera of Myrophinae lacking pectoral fins

1 Gill opening along lateral midline, a constricted opening; posterior nostril opening either along upper lip and preceded by a flap, within the mouth and covered by a flap, or entirely within the mouth; teeth varying from conical to blunt, uniserial to multiserial, all smaller than width of orbit 2

—— Gill opening more or less below lateral midline, unconstricted, its length about equal to interbranchial; posterior nostril opening entirely outside of mouth, a hole along upper lip preceded by a small flap; teeth conical and uniserial, the largest as long as the width of the orbit ..... *Skythrenchelys* n.gen.

2 Posterior nostril opens into mouth, covered partially or entirely by an exterior flap; 2 pores between nostrils; jaw teeth usually conical, uniserial or biserial, intermaxillary teeth not in a broad patch 3

—— Posterior nostril opening outside of mouth, a hole along upper lip preceded by a flap; 1 pore between anterior and posterior nostrils; teeth blunt, jaw teeth in bands; intermaxillary teeth in a patch ..... *Muraenichthys* Bleeker, 1853

3 Tongue not elongate, not extending outside of mouth, and lacking a fleshy appendage at its tip; inner edge of lips and palate smooth; teeth either conical or small and villiform, uniserial or multiserial 4

—— Tongue elongate, extending well beyond mouth and decorated with a fleshy appendage; inner edge of lips and palate decorated with fleshy lappets; teeth conical and uniserial ..... *Glenoglossa* McCosker, 1982

4 Ventral side of snout without a prominent median groove bordered by dermal folds; anterior nostrils less than eye in length 5

—— A prominent median toothed groove on ventral side of snout, bordered by dermal folds, extending anteriorly to anterior nostrils; anterior nostrils elongated tubes equal to eye in length ..... *Schismorhynchus* McCosker, 1970

5 Teeth absent on vomer, absent or embedded on intermaxillary, those on maxillary and dentary minute or villiform; dorsal-fin origin behind anus ..... *Schultzidia* Gosline, 1951

—— Teeth present on intermaxillary, maxillary, dentary and vomer; dorsal-fin origin either before or behind anus ..... *Scolecenchelys* Ogilby, 1897.

Skythrenchelys zabra n.sp.

Figs. 1A–C, 2A; Table 2

Material examined. HOLOTYPE: female, TL 239 mm, Thevara, Ernakulam, southern India, 10°00'N 76°16'E, shallow, turbid water, K.H. Mohamed, 18 July 1956, NMNZ 35152. PARATYPES: TL 234–280 mm (2), same data as holotype, NMNZ 35153; TL 256–269 mm (2, the larger cleared and stained), same data as holotype, CAS 99802; TL 259 mm (1), same data as holotype, AMS 38844-001; TL 234 mm (1), same data as holotype, BPBM 38404; TL 185 mm (1), north of Smith Point, Cobourg Peninsula, Northern Territory, Australia, 12°58'S 132°10'E, prawn trawl by N.R. Anson, 18 October 1981, NTM S.10031-004; TL 296 mm (1), Manila Bay, MUSORSTOM-Philippines 1976, station 2, trawled in 180 m, 19 March 1976, MNHN 1998-681; TL 133 mm (1), Iloilo, Panay Island, Philippine Islands, H.C. Kellers, 20 March 1929, USNM 148574; TL 119 mm (1), Straits of Malacca, 08°10'N 92°00'E, W. Gladfelter, November–December 1961, USNM 193227.

Diagnosis. A moderately elongate species of *Skythrenchelys* n.gen. with the following characters: tail 43–46% of TL; dorsal fin arising in mid-trunk; head pores: SO 1 + 4, IO 4 + 1, POM 6 + 2 or 3, ST 2; teeth conical, prominent, uniserial in jaws and on vomer; colour uniform tan. Mean vertebral formula 33.4/56.7/118.6.

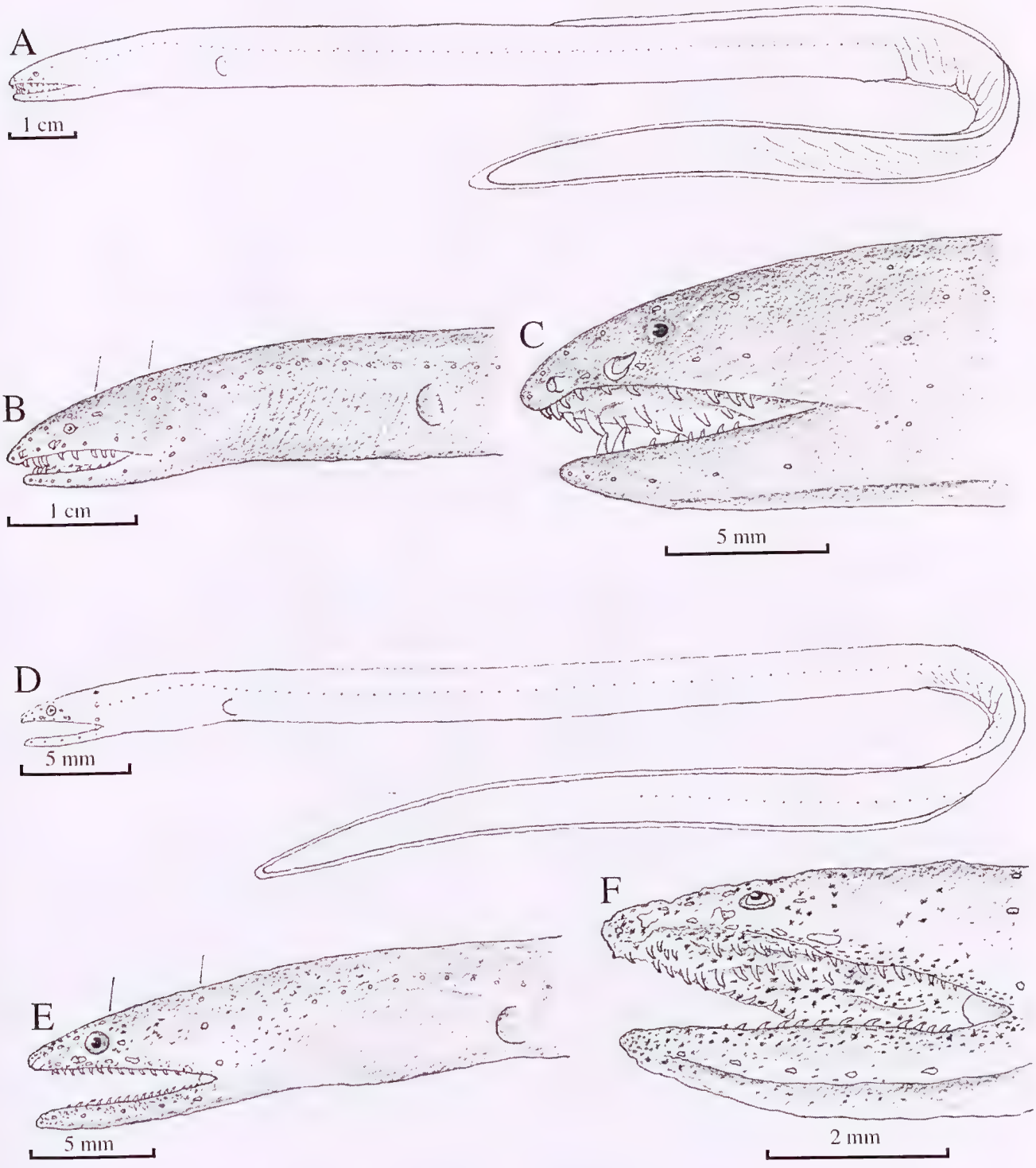

Figure 1. A–C, *Skythrenchelys zabra* n.sp., holotype, NMNZ 35152, TL 239 mm; A, body, lateral view; B, head, frontal and median supratemporal pores indicated; C, anterior part of head, ventrolateral to show intermaxillary, vomerine, maxillary and dentary teeth. D–F, *S. lentiginosa* n.sp., holotype, BPBM 29320, TL 165 mm; D, body, lateral view; E, head, median pores indicated; F, anterior part of head, ventrolateral to show intermaxillary, vomerine, maxillary and dentary teeth.

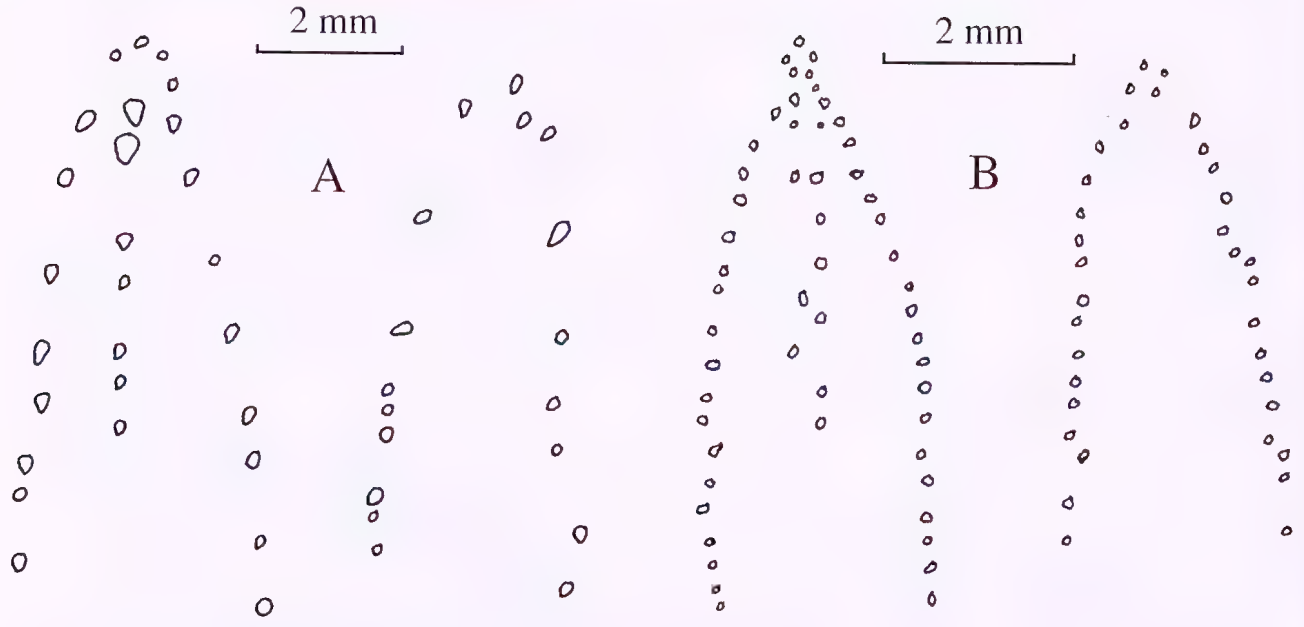

Figure 2. Patterns of upper (left) and lower (right) dentition of A—*Skythrenchelys zabra* n.sp., paratype, NTM S.10031-004, TL 185 mm; and B—*S. lentiginosa* n.sp., holotype, BPBM 29320, TL 165 mm. The sketches show arrangement, number and general size of the teeth, not their shape.

Further description. Measurements of holotype in mm. Total length 239; head length 31.9; trunk length 100.6; tail length 106.5; body depth at gill opening 8.9; body width at gill opening 4.5; body depth at anus 8.3; origin of dorsal fin 80.5; gill opening length 3.9; gill opening interspace 4.5; snout length 4.1; upper jaw length 9.0; eye diameter 1.0; interorbital space 3.1. Dorsal rays before anus 69; total dorsal rays 230; total anal rays 164. Lateral line pores before dorsal origin 35; total lateral line pores 105. Vertebral formula 34/57/116. Proportions and counts of holotype and 8 paratypes are presented in Table 2.

Body only moderately elongate (Fig. 1A), slender, rounded in section along most of its length, depth at gill opening 27 (25–36) in TL, head and trunk 1.8 (1.7–1.8) and head 7.5 (7.1–7.9) in TL. Snout pointed, depressed, its tip turned downwards over tip of lower jaw. Jaws elongate, curved, incapable of closing completely, lower jaw little shorter than snout. Mouth cleft reaching to well beyond eye; lower lip with irregular ridges on its inner surface alongside dentary teeth. Anterior nostril subterminal, a short tube, its rim simple; posterior nostril before and below eye, above free edge of upper jaw, a fully exposed, oblique slit with a free flap on its anterior and ventral rim, the anterior portion being much more prominent and the flap tending to form an anteroventral channel leading downwards to upper edge of mouth (Fig. 1C). Eye very small, diameter 31.9 (26.1–38.0) in head. Interorbital moderately broad. Gill opening crescentic, midlateral, relatively large. Pectoral fin a scarcely visible, extremely weak ridge behind gill opening, supported by several minute rays, the bases of which are visible in the base of the ridge and which project slightly from the free edge. Median fins low, anal fin height less than dorsal. Dorsal fin origin about halfway between gill opening and level of anus. Caudal fin short.

Head pores present and obvious (Fig. 1B), in holotype and 2 NMNZ paratypes on each side as follows: SO 1 + 4, IO 4 + 1, POM 6 + 3 (the 2 CAS paratypes have 2 preopercular pores), ST 2. Lateral line pores present, absent along posterior third of tail.

All teeth prominent (Figs. 1C, 2A), sharp, recurved, relatively few, uniserial and widely separated; in the holotype 2 large and 7 smaller on vomer; 8–9 on maxilla and dentary of which front 2–3 are larger than remainder; 2 or 3 on intermaxillary.

Body colour in isopropyl alcohol light greyish tan, lighter below, with very scattered minute freckles on dorsum of head and snout. Life colour unknown.

Gill arches not well developed; basibranchials absent, hypobranchials 1–2 ossified, hypobranchial 3 absent, ceratobranchials 1–4 ossified, ceratobranchial 5 absent; upper pharyngeal tooth plates closely sutured but not fused, with 17–18 conical teeth; lower pharyngeal tooth plate slender, smaller than upper plates, with 14–15 conical teeth.

Distribution and biology. India, Straits of Malacca, Philippines, Indonesia and northern Australia. Holotype—a female with 0.4 mm ova; all paratypes from Ernakulam (India) are females, except one possible male. The Ernakulam inlet is a large, shallow, turbid estuary; the other localities are apparently much the same, except that the Manila Bay specimen was collected in deeper water.

Etymology. From Greek *zabros* (gluttonous), in reference to the ability of this eel to ingest very large prey (as evident from radiographs of two paratypes [NMNZ 35153, 280 mm TL; MNHN 1998-681, 296 mm TL] that have enormous fish specimens filling out much of the gut cavity). The specimens were caught by fine-mesh

Table 2. Proportions (in thousandths) and counts of the holotype and eight paratypes of *Skythrenchelys zabra* n.sp. Abbreviations: TL = total length, HL = head length, DFO = dorsal fin origin, GO = gill opening, IO = interorbital space; number of specimens in parentheses.

	holotype	mean	range
total length, mm	239	—	119–296
head/TL	133	132.4	127–137
trunk/TL	421	423.6	406–468
tail/TL	446	444.0	405–457
depth at GO/TL	37	34.3	28–40
depth at anus/TL	35	26.7	24–30
DFO/TL	336	332.5	314–356
GO length/HL	122	99.4	81–134
GO interspace/HL	141	135.7	100–162
snout/HL	129	119.8	107–149
upper jaw/HL	282	298.1	252–379
eye/HL	31	30.5	26–38
IO/HL	97	86.8	74–110
dorsal-fin rays			
before anus	69	72.4	64–80
total rays (6)	230	233.3	217–250
anal-fin rays	164	150.1	127–165
lateral-line pores			
before DFO (7)	35	33.9	32–36
before anus (7)	58	56.4	55–57
total pores	105	92.8	90–99
vertebrae			
predorsal	34	33.4	31–36
preanal	57	56.7	55–58
potal	116	118.6	112–122

set net (NMNZ 35153) and by bottom trawl (MNHN 1998-681). That the prey might have been scavenged by the eels from the contents of the nets has to be considered, though the possibility is remote.

Skythrenchelys lentiginosa n.sp.

Figs. 1D–F, 2B

Material examined. HOLOTYPE: female, TL 165 mm, Red Sea, Port Sudan Harbour, 19°38'N 37°07'E, 25 m, rotenone, R. Lubbock and P. Etherington-Smith, 30 July 1972, BPBM 29320.

Diagnosis. A moderately elongate species of *Skythrenchelys* n.gen. with the following characters: tail 51% of TL; dorsal fin arising above anus; pores SO 1 + 4, IO 4 + 1, POM 6 + 1 or 2, ST 2; teeth conical, well-developed, uniserial in jaws and biserial in anterior vomer region; anterior head region and inside of mouth overlain with numerous brown freckles. Vertebral formula 51/50/120.

Further description. Measurements of holotype in mm. Total length 165; head length 20.3; trunk length 60.7; tail length 84; body depth at gill opening 4.6; body width at gill opening 4.2; body depth at anus 3.8; body width at anus 3.5; origin of dorsal fin 84; gill opening length ≈1.9; gill opening interspace ≈3.4; snout length 2.5; upper jaw length 7.4; eye diameter 0.8; interorbital space 1.65. Total dorsal rays 208; total anal rays 187. Lateral line pores before anus 50.

Body only moderately elongate (Fig. 1D), robust and nearly round in trunk and anterior tail region, tapering and laterally compressed posteriorly; depth at gill openings 36 in TL; head and trunk 2.0 and head 8.1 in TL. Snout acute, slightly bulbous at tip, without a median groove on its underside. Jaws elongate, curved, incapable of closing completely; centre of eye in anterior 1/3 of upper jaw; lower jaw included, its tip in advance of anterior nostrils. Anterior nostril subterminal, a short tube, its rim simple; posterior nostril entirely outside upper lip, beginning before anterior margin of eye, appearing externally as a large pore with a

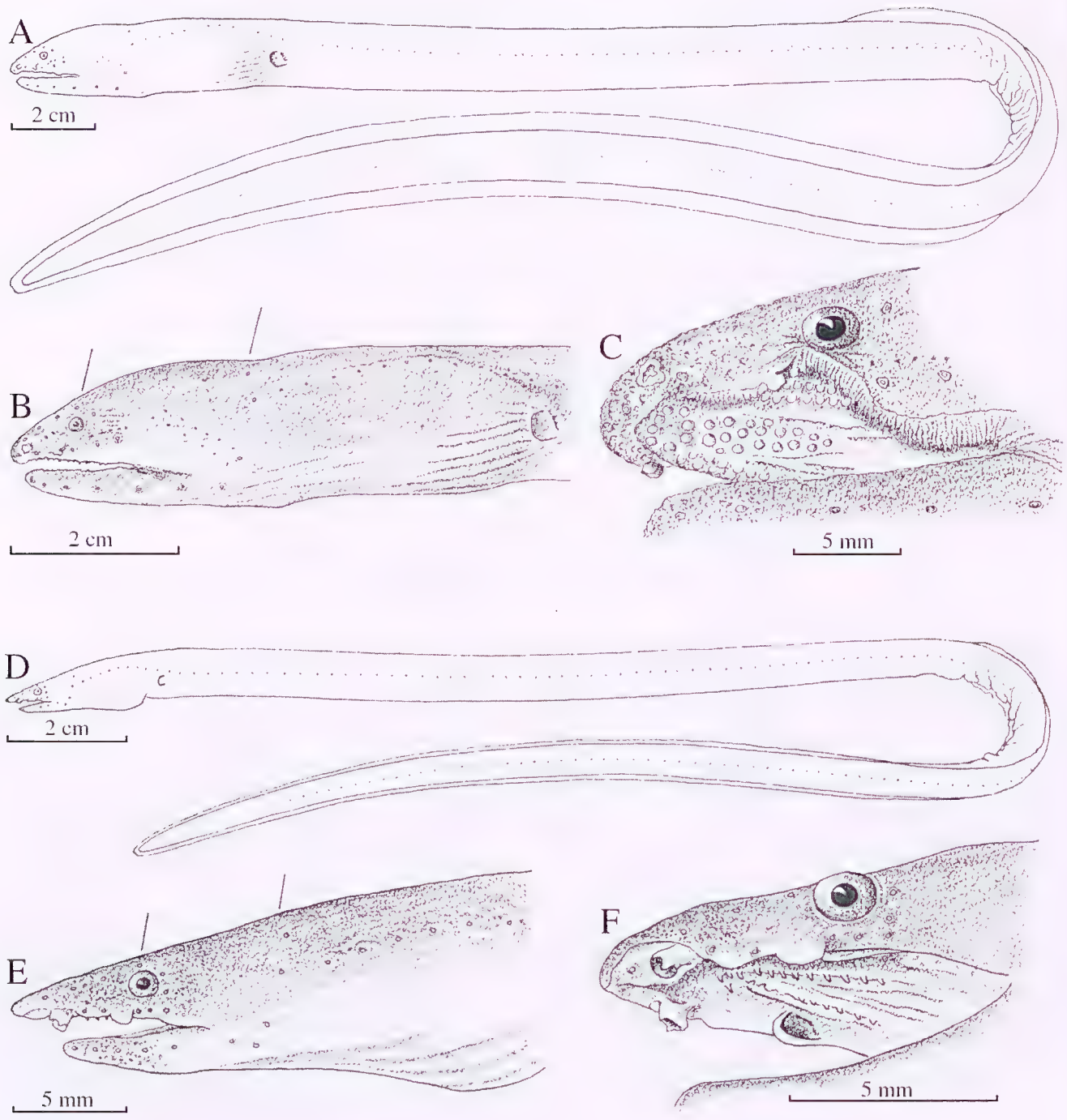

Figure 3. A–C, *Muraenichthys gymnopterus*, BPBM 32816, TL 497 mm; A, body, lateral view; B, head, median pores indicated; C, anterior part of hefad, ventrolateral to show vomerine and maxillary teeth (upper lip turned back). D–F, *Scolecenchelys australis*, NMNZ P.13230, TL 341 mm; D, body, lateral view; E, head, median pores indicated; F, anterior part of head, ventrolateral to show vomerine and maxillary teeth.

small, anterior flap. Eye small, diameter 25.3 in head and about twice in interorbital distance. Interorbital region dome-shaped. Pectoral fins absent. Median fins low, confluent with caudal. Dorsal fin origin above level of anus. Caudal fin very short.

Head pores mostly large and obvious (Fig. 1E), but those of preoperculomandibular series difficult to ascertain and subject to confirmation with the collection of larger specimens; SO 1 + 4, IO 4 + 1, POM 5 + 1 or 2, ST 2. A single pore between anterior and posterior nostrils. Four pores along mandible, 1 or 2 overlying preopercle. Lateral line pores not apparent along posterior third of tail region; approximately 10 pores above branchial basket.

Teeth conical, recurved, and large compared to most myrophines (Figs. 1F, 2B). An anterior intermaxillary block of 5 small teeth, followed by 3 large teeth and a smaller pair of teeth, followed by a uniserial but nonlinear row of 9 vomerine teeth decreasing in size. Maxillary teeth uniserial, 17–18 in a row, decreasing in size. Mandibular teeth uniserial, about 5 smaller teeth near symphysis, followed by 15–16 larger teeth decreasing in size.

Body colour in isopropyl alcohol uniform tan; snout, jaws chin, lips and inside of mouth with many brown to black freckles; numerous fine brown punctations occur above lateral midline; median fins pale; eyes dark blue. Life colour unknown.

Distribution and biology. Known only from the holotype, from the Red Sea. The holotype is a small female with developing ova of 0.3–0.4 mm in diameter; most ophichthids of this size are sexually immature.

Etymology. From Latin *lentiginosus* (freckled), in reference to the speckled head coloration.

Affinities of the two species. After discovering this remarkable specimen in the BPBM collection, McCosker was reluctant to describe it as a new genus and species until larger specimens were discovered. With the collection of many and larger specimens of its congener, *S. zabra* n.sp., we now feel confident in proceeding with its description. The two new species of *Skythrenchelys* n.gen. are easily separable externally on the basis of the origin of their dorsal fin, eye size and dentition (*S. zabra* n.sp. having the dorsal origin further forwards, a much smaller eye and relatively larger teeth), and minor differences in body/tail proportions and dentition. *Skythrenchelys zabra* n.sp. has distinctively large teeth and *S. lentiginosa* n.sp. would not be mistaken for any other ophichthid on the basis of its extraordinary jaw elongation, dentition, and facial coloration.

It is unknown if the coloration of *S. lentiginosa* n.sp. is maintained as it grows, though some facial spotting is likely to remain or even be enhanced with growth. Its facial coloration, eye position, jaw size and developed dentition would suggest a hole-dwelling habitus with only its snout and eyes exposed as is also likely for *S. zabra* n.sp. Such an appearance and lie-in-wait behaviour is typical of species of ophichthine genera such as *Brachysomophis* Kaup, 1856 and *Echiophis* Kaup, 1856 (McCosker *et al.*, 1989).

On the status of *Muraenichthys* and *Scolecenchelys*

As stated in our introduction, several authors (Schultz & Woods, 1949; Gosline, 1951; McCosker, 1970, 1977) have recognised the polyphyletic nature of the many species assigned to *Muraenichthys* but were disinclined to identify the species groups as belonging to separate genera. We have seen most of the type specimens and are confident of the adequacy of most recent descriptions to thereby allow us to divide *Muraenichthys* into two separate phyletic groups. They are separable on the basis of characters described in the key and in Table 1. Specimens of the type species of *Muraenichthys* and *Scolecenchelys* are illustrated in Fig. 3. Aspects of the osteology of *Muraenichthys gymnopterus, Scolecenchelys chilensis, S. gymnotus* and *S. macropterus* are described and illustrated in McCosker (1977).

We provisionally list below the species that we consider to comprise the two genera; the species and their authors are listed in Eschmeyer (1998).

Muraenichthys (type species *Muraena gymnopterus* Bleeker, 1853) includes the following: *Muraena gymnopterus* (and its synonyms *Muraenichthys hattae* Jordan & Snyder, 1901 and *Muraenichthys microstomus* Bleeker, 1865); *Muraenichthys macrostomus* Bleeker, 1865; *Muraenichthys schultzei* Bleeker, 1857; *Muraenichthys sibogae* Weber & de Beaufort, 1916; and *Muraenichthys thompsoni* Jordan & Richardson, 1908 (and its probable synonyms *Muraenichthys malabonensis* Herre, 1923, the type apparently destroyed, and *Muraenichthys philippinensis* Schultz & Woods, 1949).

Scolecenchelys (type species *Muraenichthys australis* Macleay, 1881, by original designation), and its synonyms *Myropterura* Ogilby, 1897 (type species *M. laticaudata* Ogilby, 1897, by original designation) and *Aotea* Phillipps, 1926 (type species *A. acus* Phillipps, 1926, by monotypy) includes the following: *Muraenichthys acutirostris* Weber & de Beaufort, 1916; *Muraenichthys australis* Macleay, 1881 (and probable synonyms *Muraenichthys iredalei* Whitley, 1927, *Muraenichthys lengomena* Scott, 1980, *Muraenichthys lingowenah* Scott, 1975, and *Muraenichthys oliveri* Waite, 1910); *Muraenichthys borealis* Machida & Shiogaki, 1990; *Muraenichthys breviceps* Günther, 1876 (and synonyms *Aotea acus* Phillipps, 1926, *Muraenichthys devisi* Fowler, 1907, and *Muraenichthys ogilbyi* Fowler, 1907); *Muraenichthys chilensis* McCosker, 1970; *Muraenichthys cookei* Fowler, 1928; *Muraenichthys erythraeensis* Bauchot & Maugé, 1980; *Muraenichthys godeffroyi* Regan, 1909 (and probable synonym *Muraenichthys elerae* Fowler, 1934); *Muraenichthys gymnotus* Bleeker, 1857 (and synonyms *Muraenichthys aoki* Jordan & Snyder, 1901, *Muraenichthys fowleri* Schultz, 1943, and *Sphagebranchus huysmani* Weber, 1913); *Muraenichthys japonicus* Machida & Ohta, 1993; *Myropterura laticaudata* Ogilby, 1897; *Muraenichthys macropterus* Bleeker, 1857 (and synonyms *Muraenichthys owstoni* Jordan & Snyder, 1901 and *Echidna uniformis* Seale, 1901); *Muraenichthys nicholsae* Waite, 1904; *Muraenichthys okamurai* Machida & Ohta, 1996; *Muraenichthys profundorum* McCosker & Parin, 1995;

Muraenichthys puhioilo McCosker, 1979; *Muraenichthys tasmaniensis* McCulloch, 1911 (and synonym *M. tasmaniensis smithi* Whitley, 1944); *Chilorhinus (Muraenichthys) vermiformis* Peters, 1866; and *Muraenichthys xorae* Smith, 1958. *Incertae sedis*: *Muraenichthys moorii* Günther, 1870. Note that adjectival suffixes of species transferred from *Muraenichthys* to *Scolecenchelys* will change, in that *enchelys* is feminine.

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A New Species of the Devonian Lungfish *Dipnorhynchus* from Wee Jasper, New South Wales

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ABSTRACT. A new large mandible of *Dipnorhynchus* from the Early Devonian *serotinus* Zone (late Emsian) at Wee Jasper, is given the status of a new species, *D. cathlesae* n.sp. This fossil characterised by its size; relative depth with respect to its length; short anterior furrow, deeply bordered by a raised broad rim of dentary between itself and the labial pit; large foramen for a nerve in the posteromedial end of the labial furrow; a strong furrow from the adductor pit to the posterior end of the labial pit; thick dentary; lack of tubercles (blisters) on the prearticular plate; and an adductor pit wide posteriorly and narrowing gradually anteriorly. The surface of the tooth plate is not made of dentine, but of bone formed on the surface of the prearticular. This species represents the youngest known occurrence of *Dipnorhynchus* in the Murrumbidgee sequence.

CAMPBELL, K.S.W., & R.E. BARWICK, 1999. A new species of the Devonian lungfish *Dipnorhynchus* from Wee Jasper, New South Wales. *Records of the Australian Museum* 51(2): 123–140.

Early Devonian dipnoans were beginning a period of rapid evolution. The number of species is limited at present, but many of them are beautifully preserved in limestone, and can be extracted as three dimensional fossils with acetic acid. The specimens from Wee Jasper on the Burrinjuck Dam, New South Wales, are among those that have produced the best information on undistorted material. *Dipnorhynchus* is the most abundant of these genera. Herein we describe a new species of *Dipnorhynchus, D. cathlesae*.

The limestone-shale sequence at Wee Jasper and Taemas covers a range from the *dehiscens* Zone to the *serotinus* Zone of the Emsian. The rocks are more or less continuously fossiliferous and include many marine invertebrate fossils including corals and brachiopods. Remains of the dipnoan *Dipnorhynchus* have been previously described from several levels at both Taemas and Wee Jasper, but a recent discovery of a mandible of this genus towards the top of the sequence provides information on its subsequent evolution. The specimen was discovered by Ian and Helen Cathles of Cookmundoon Station, Wee Jasper.

Most of the rocks were deposited in shallow subtidal environments, but occasional supratidal deposits are also found. All the specimens of *Dipnorhynchus* were found in the subtidal limestones.

The specimen herein described shows large neural openings into a labial pit, the outer edge is formed by a high margin of the surangular; reduced dental structure (tubercles) on the prearticular; and the great height of the

Table 1. Comparison between the dimensions of the holotype of *Dipnorhynchus cathlesae* and the largest known specimen of *Dipnorhynchus kurikae* Campbell & Barwick (ANU 60030).

species	width at mandibular articulation (cm)	length (cm)	maximum depth of mandible (cm)	maximum depth of dentary (cm)
D. cathlesae	22	19	10	6.5
D. kurikae	15	14	5.5	3

posterior face of the mandible leaving a shallow space for the tongue mass. We interpret these features to mean that the suction capacity of the animal was increased beyond what is shown by the earlier species, that the tooth plates were modified to be crushers of food, and that the capacity of the hyoid apparatus to move forward and backwards was greatly reduced.

This specimen is so large that when it was first observed in the rock, it was not recognised as a dipnoan. The major dimensions are outlined above (Table 1), and are set against the largest known specimen of *D. kurikae* (Campbell & Barwick, 1985). Note that *D. kurikae* is dwarfed by the specimen of *D. cathlesae*, especially in its depth.

The specimen was exposed on the rock surface and its posterior face was weathered. It was collected in five fragments, four of which were in association and one was isolated. The associated fragments were separated by cracks and breaks in the rock, and they fell apart on collection. Reassembly showed that fragments of bone were missing from some of the edges, but by and large the fragments could be restored sufficiently to permit us to make a description of most of the osteological features. The isolated

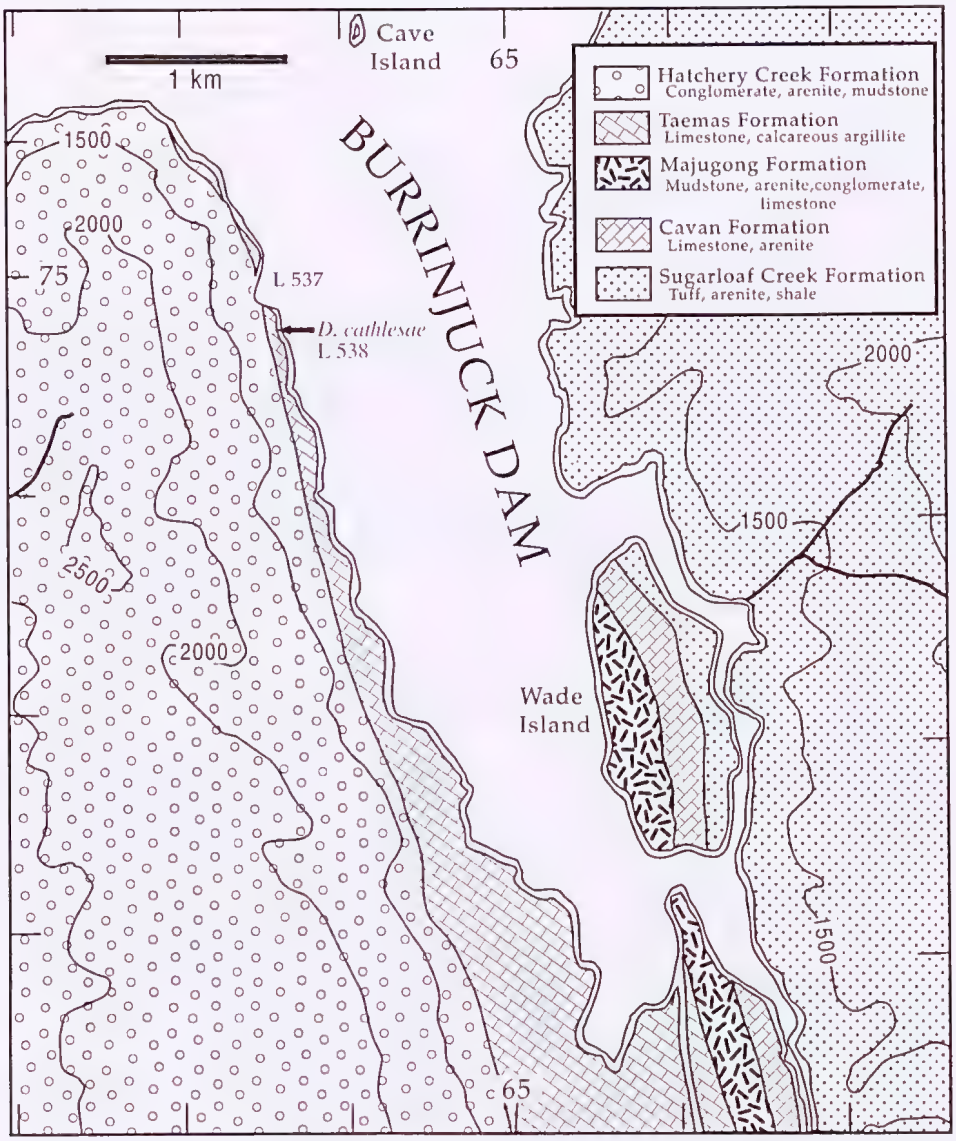

Figure 1. Map of the northern part of the Wee Jasper outcrop of the Lower Devonian Limestones, modified after Pedder *et al.* (1970). The numbers L 537 and L 538 refer to the collection data of Pedder *et al.*

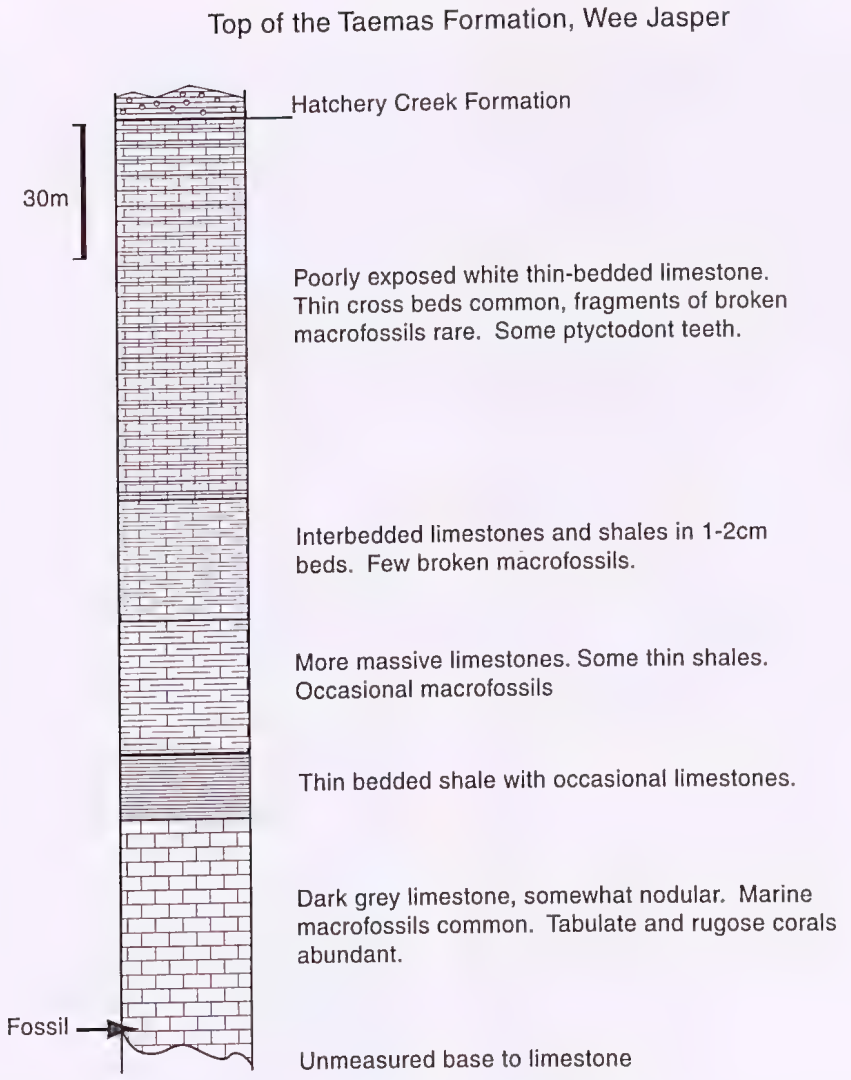
Top of the Taemas Formation, Wee Jasper
Hatchery Creek Formation
30m
Poorly exposed white thin-bedded limestone. Thin cross beds common, fragments of broken macrofossils rare. Some ptyctodont teeth.
Interbedded limestones and shales in 1-2cm beds. Few broken macrofossils.
More massive limestones. Some thin shales. Occasional macrofossils
Thin bedded shale with occasional limestones.
Dark grey limestone, somewhat nodular. Marine macrofossils common. Tabulate and rugose corals abundant.
Fossil
Unmeasured base to limestone

Figure 2. Stratigraphic section measured from the locality where *Dipnorhynchus cathlesae* was collected up to the Hatchery Creek Formation.

fragment was found down slope from the original specimen, and consists of a piece of a mandible that fits a section missing from the original. No other bone fragments are found in the vicinity and the bone size in the fragment matches the main specimen.

In the absence of other bones in the sediments around the point where the specimen was recovered, and despite several detailed searches in the surroundings, which are well exposed because the withdrawal of the waters of the Burrinjuck Dam in the 1998 drought, we conclude that any other specimens of the species that lived in the area have not been preserved in observable rocks. In the sediments overlying the specimen there are several layers of limestone containing ptyctodont fragments, but these rocks have not yielded any large fragments of bone.

Stratigraphy

A map showing where the specimen was collected is given in Fig. 1, and the stratigraphic sequence of the upper part of the Taemas limestone at Wee Jasper is presented in Fig. 2.

The uppermost unit below the Hatchery Creek Formation consists of very thin bedded white limestones, many beds being only 1 mm thick. The unit is c. 69 m thick. Some crossbedding is present. The rocks are interpreted as an intertidal zone carbonate deposit, which is consistent with the fact that the overlying unit is the fresh water Hatchery Creek Formation. The limestone has few invertebrate macrofossils, but ptyctodont tooth plates are occasionally present.

Immediately beneath this unit are three strata consisting of interbedded limestones and shales. These contain few macrofossils, but occasionally they have a few ptyctodonts. Together these three units are c. 58 m thick.

Our specimen comes from c. 40 m below the top of the limestone beneath the above mentioned three units, near the locality listed as by Pedder *et al.* (1970) as L538 at the northern end of the Taemas limestone outcrop. This lower limestone is different in kind from those lying above it, being a dark grey colour, often nodular, and in units some centimetres thick. It was deposited in an environment which supported a rich marine life. The commonest fossils are the thamnoporoid and favositid tabulates associated with an

abundant ceroid syringoporoid probably related to *Romeripora* (Hill & Jell, 1970). The corals are all rolled and show a variety of shapes, indicating that at least during the final depositional event, a rough water environment existed. The rugosans have been described by Pedder in Pedder *et al.* (1970), and fig. 4 of that paper lists seven species of corals which are restricted to this level. Garratt & Wright (1989) have indicated that this unit belongs to their Coral Zone F. The conodonts were also described by Philip & Jackson in Pedder *et al.* (1970), and subsequent work outlined by Basden *et al.* (1999) indicates that they belong to the *serotinus* Zone of late Emsian age. Other fossils in the dipnoan bearing limestone include stromatoporoids and gastropods. Brachiopods are rare. The fossil site is c. 142 m beneath the Hatchery Creek Formation.

One peculiarity of the occurrence is the fact that no other bone was found anywhere in the vicinity. In the Wee Jasper sequence, fragments of placoderms are commonly found near dipnoans, but prolonged searches at this locality failed to find bone of any kind.

The locality is on the flank of the syncline of which the axis lies nearby. Hence the rocks have been subject to the cleavage which is common in the area, and the dipnoan specimen is somewhat distorted. Despite this the specimen restoration is not badly deformed.

Systematic palaeontology

Genus *Dipnorhynchus* Jaekel, 1927

Type species. *Ganorhynchus sussmilchi* Etheridge Jr., from the *Spinella yassensis* Limestone at Taemas, Burrinjuck Dam, New South Wales.

Remarks. Although we have no skull of the new species described herein, we confidently assign the mandible to *Dipnorhynchus*. It displays the main features of the mandible of that genus, and it has no evidence of teeth on the prearticulars which should be there if it were related to *Speonesydrion*, the only other genus of dipnoans found in this stratigraphic sequence.

The specimen was prepared by etching with acetic acid, so that much of the internal structure which is not visible on other more complete dipnorhynchids, was directly observable on this specimen. To hold some of the more fragile parts in position, thin wooden struts were placed in position, and these can be seen on Fig. 3.

Dipnorhynchus cathlesae n.sp.

Holotype. ANU60027, from the upper part of the Taemas limestone, near L538 on the map of Pedder *et al.* (1970). Specimen on loan from I. & H. Cathles, Cookmundoon Station, Wee Jasper.

Diagnosis. Large species with its height relative to length greater than in any other members of the genus; dentary with a high lateral edge; labial pit deep and bordered by a high margin composed of the surangular; large neural connection from the adductor cavity to the labial pit; a large groove extends from the adductor pit to the labial pit; lingual space very shallow; no tubercles (blisters) on the prearticular tooth plate.

Remarks. Our first reaction was that the specimen was a large adult of *D. kurikae*, a species found in the *Receptaculites* and at the top of the Bloomfield Limestone, lower down in the stratigraphic sequence. The largest specimen of that species we have collected is a palate described by Campbell & Barwick (1985: fig. 5), but it is smaller than the present specimen. A number of characters found in this new specimen are of the same kind as those found in other dipnorhynchid species, but their proportions differ. On the other hand, some features are different in kind from what are known elsewhere. For these reasons we have decided to describe the specimen as a new species. We now refer to the individual characters separately.

1. In comparison with other dipnorhynchids, the **labial pit** (Figs. 5, 6B–D, 10) is a short deep structure. Its lateral edge, formed from the surangular, is high and makes a distinct margin, turned inwards along its dorsal edge and slightly overhangs the pit. Posteriorly, this edge rises up to join the edge of the surangular forming the outer edge of the adductor fossa, leaving a groove (a labial groove, Figs. 4A, 10) along the inner face of that bone. This labial groove, which is up to 6 mm in diameter, runs from the anterior margin of the adductor fossa into the lowermost margin of the labial pit. It can be traced along the inner face of the dermal bones for about 2 cm posterior to the anterior end of the adductor fossa, gradually becoming less clear posteriorly. The inturned edge of the dermal bone which overhangs it is covered by fine granules as are common along the more posterior edge of the surangular. The breadth of this granulated area is narrower than is found in specimens of *D. kurikae*.

In its depth and continuity into the adductor chamber this groove is unlike any structure which we have observed in other dipnorhynchids. In *D. kurikae*, the labial pit is shallow and does not have an upturned lateral margin. In *D. sussmilchi* the labial pit is even shallower, and its lateral margins are downturned rather than forming a rim. In *D. kurikae* a slight groove is present running along the floor of the labial pit and, running along the flattened surface of the bone behind the labial pit, it enters the adductor fossa at its *anteromedial* end. This is the boundary between the surangular and the bone forming the remainder of the floor of the labial pit. Clearly this cannot make any impression on the inner face of the surangular, and it is not in the same position as the groove in *D. cathlesae*.

Did this groove in *D. cathlesae* house a vessel, or a nerve, or a muscle or a ligament? We do not accept that it was a nerve because of its size, and because the abundant supply of nerves observed elsewhere in the labial pit make the same pattern we have observed in other dipnorhynchids (Thomson & Campbell, 1971: figs. 20, 41, 80; Campbell & Barwick, 1985: figs. 8a, 9a). In particular a large foramen at the *posteromedial* end of the labial pit passes outward from the adductor chamber through bone beneath the posterior end of the dentary. This carried a nerve from the adductor chamber to the labial pit; it also carried a branch which turns forward into the posterior end of the anterior

fossa. Because it carries the two branches, the foramen at the posterior end of the labial pit is obviously double internally but apparently single externally. The foramen joins the labial pit and the longitudinal groove by a deep furrow on the right side of the specimen, but on the left the furrow is much shallower, and has a small anteriorly directed furrow opening out of its margin. In extant dipnoans, only nerves V and VII extend forwards to this position. These would have supplied the sensory nerves to the soft tissues in the anterior furrow and the labial pit. Other nerves which enter the labial pit pass into the base of the pit via a large number of foramina (Figs. 6C,D). These open down into the adductor cavity, and they would have carried nerves and vessels which entered the labial pit. Thus we can account for a nerve and blood supply to the lip, and so there is no need for a large nerve or the provision of a blood supply from the adductor chamber through the foramen under discussion.

Therefore this labial groove must have carried a muscle or a ligament from the adductor pit to the lip. The lips of extant lungfish take an active part in the feeding mechanism (Bemis, 1987, for summary). In his comments on the lips and tongue, Bemis noted that chondroid tissue plays an important part in outlining the shape of the lips. In *Lepidosiren*, the upper and lower lips engage each other to make a surface against which the inflow of water can be controlled. *Protopterus* has a different and more complicated system. We have no reason to think that our new primitive form followed either of these patterns, but the presence of large lip spaces suggests that the ability to be a suction feeder was already present in the Devonian. Other dipnorhynchids did not have a large groove running into the labial pit as does *D. cathlesae*, and yet they probably possessed a suction feeding capacity. Hence we conclude that the capacity to produce suction feeding was present without the structure in the groove in question. However, the fact that the lips are known to be of major importance for suction in extant dipnoans, and different means for improving suction were evolved by different extant genera, it seems reasonable to infer that *D. cathlesae* had developed an improved method for suction in comparison with previous members of the genus.

As the groove runs posteriorly into the adductor fossa where it loses contact with the dermal bone and would have been adjacent to the adductor muscles, the soft tissue could have contained an offshoot from the adductor musculature. This is of interest because the lip retractor muscles of *Lepidosiren* and *Protopterus* are derived embryologically from the adductor mass (Bemis, 1987: 262). On the other hand, the groove could have contained chondroid tissue connected into the adductor muscle chamber. The information we have at present does not allow us to choose between these two hypotheses.

2. In all dipnorhynchids, the well-defined **anterior furrow** (Figs. 4A, 7A,B) is completely surrounded by bone in dorsal view. It is bounded anteriorly and laterally by the dentary, and posteriorly by the prearticular. In all the other known species of dipnorhynchids, the anterior furrow is long and narrow. In some specimens it is divided by the prearticular joining the dentary medially, but the distribution of this feature among populations shows that it is subject to intraspecific variation. In *D. cathlesae* the anterior furrow is present and is enclosed in the usual way for a dipnorhynchid, but it is shorter and wider in dorsal view than in other dipnorhynchids. Part of this may be due to the fact that the prearticular extends slightly over its posterior end. Despite this, the furrow is less than two-thirds the length of the dentary.

The anterior end of the furrow is overhung by the dentary which turns down into the furrow, and is bounded by a strong ridge parallel with the anterior edge of the furrow. Medially on this edge there is a narrow thin protrusive layer which has the appearance of dentine. Deeper into the furrow, the dentary forms a groove which is bounded ventrally by a thin line where it joins the endoskeletal bone. On the posterior face of the anterior furrow the dental plate overhangs, leaving a groove. This groove is at about the same level as the groove in the dentary around anterior furrow mentioned above. We conclude that a layer of soft tissue formed within the anterior furrow, protecting the soft (sensory) tissue filling the lower part of the anterior furrow. Presumably this covering layer must have contained many perforations to permit interaction with the sensory tissue beneath. From its position we think that it was a chemosensory structure at the entrance to the mouth.

The floor of the furrow is formed of open textured endoskeletal bone which contains several foramina. These foramina (Figs. 7A,B) are present on both sides of the specimen, though they are differently disposed with respect to the mid-line. This is normal for dipnorhynchids (Campbell & Barwick, 1985). The right side of the specimen has at least six large foramina similarly opening downwards into either the anterior end of the adductor chamber, or the space occupied by tubules between the adductor chambers.

The posterolateral corners of the anterior furrow are strongly overhung by the edge of the prearticular dental plate. High up in the posterolateral corner of the anterior furrow is a foramen which opens via a long tube, which is entirely concealed in bone, into one of the foramina making up the large unit at the posterior end of the labial pit (Fig. 10). The second foramina in this unit also sends a nerve into the posterior end of the labial pit. This nerve would have been either V or VII, as comparison with *Speonesydrion iani* shows (Campbell & Barwick, 1984: fig. 25).

3. The **dentary** (Figs. 4A, 6B–D, 10) is much thicker dorsoventrally than that of any other dipnorhynchid. Ventrally it is not separated from the infradentaries by the slight groove which is common on all other dipnorhynchids, but it grades smoothly into the infradentaries. Along its dorsal surface the median part is smooth, depressed beneath the levels of the lateral parts, and does not support a transverse ridge. Laterally the dentary is also well rounded on its dorsal surface, and the surface continues forward to the level of the anterior end of the anterior furrow. In other dipnorhynchids the lateral surface of the dentary decreases height more posteriorly. In *D. kurikae* at all stages of growth, the dentary has a secondarily thickened ridge along the lateral crest. No sign of such a ridge is present in *D. cathlesae*. Nor is there present a thickened ridge along the anterior margins of the dentary making a distinct feature in *D. kurikae*.

Figure 3. A, ventral and B, dorsal views of the holotype of *Dipnorhynchus cathlesae*. Photographs are greatly reduced in size. Arrow indicates where sections shown on Figs. 11–14 were cut. Isolated left fragment not included in figure, see Fig. 4. Scales = 1 cm.

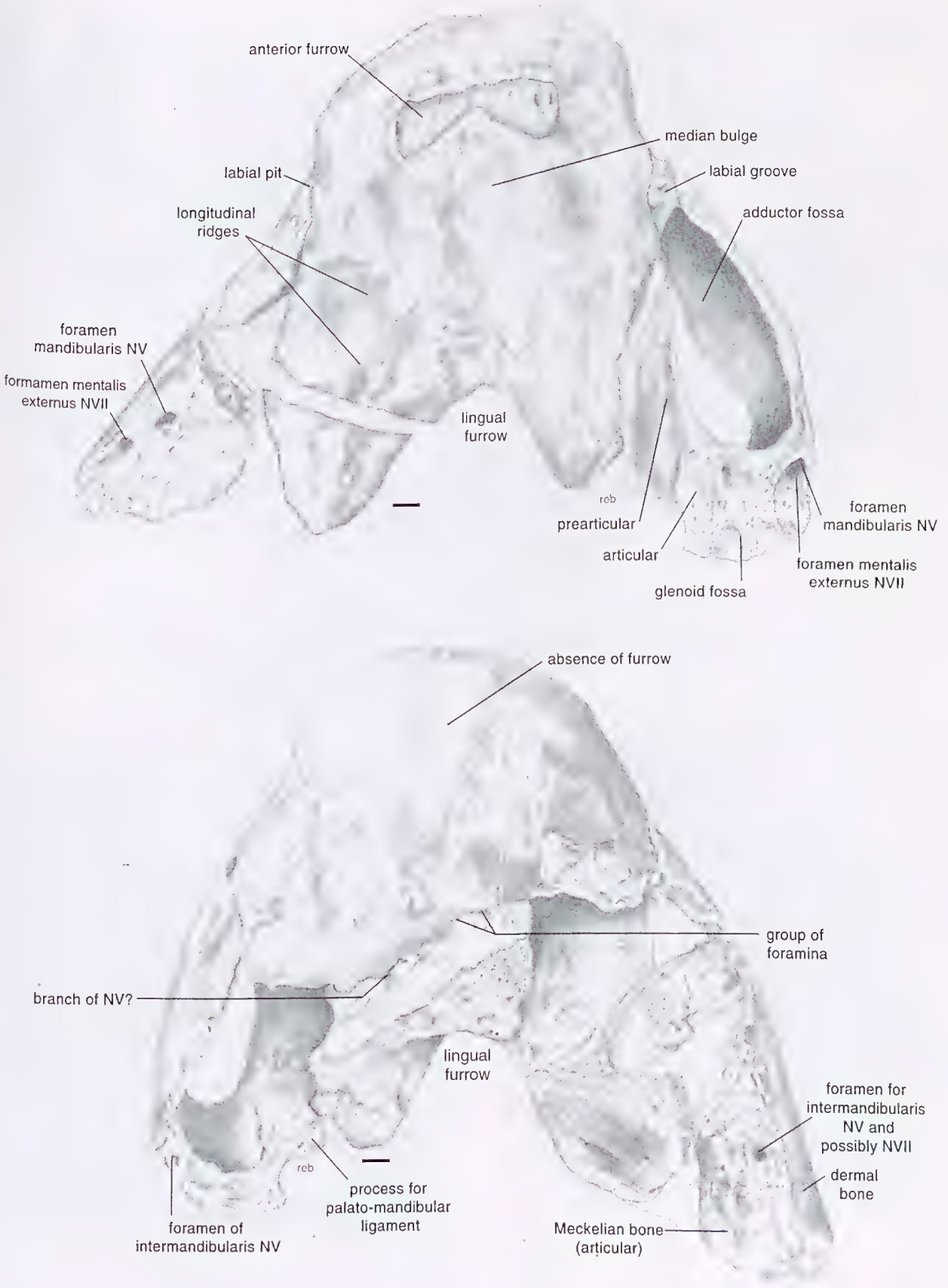

Figure 4. Reconstruction of the mandible of *Dipnorhynchus cathlesae* in dorsal and ventral views. The isolated part in the left side of the specimen did not fit back perfectly, and are shown in two slightly different positions on A and B. Scales = 1 cm.

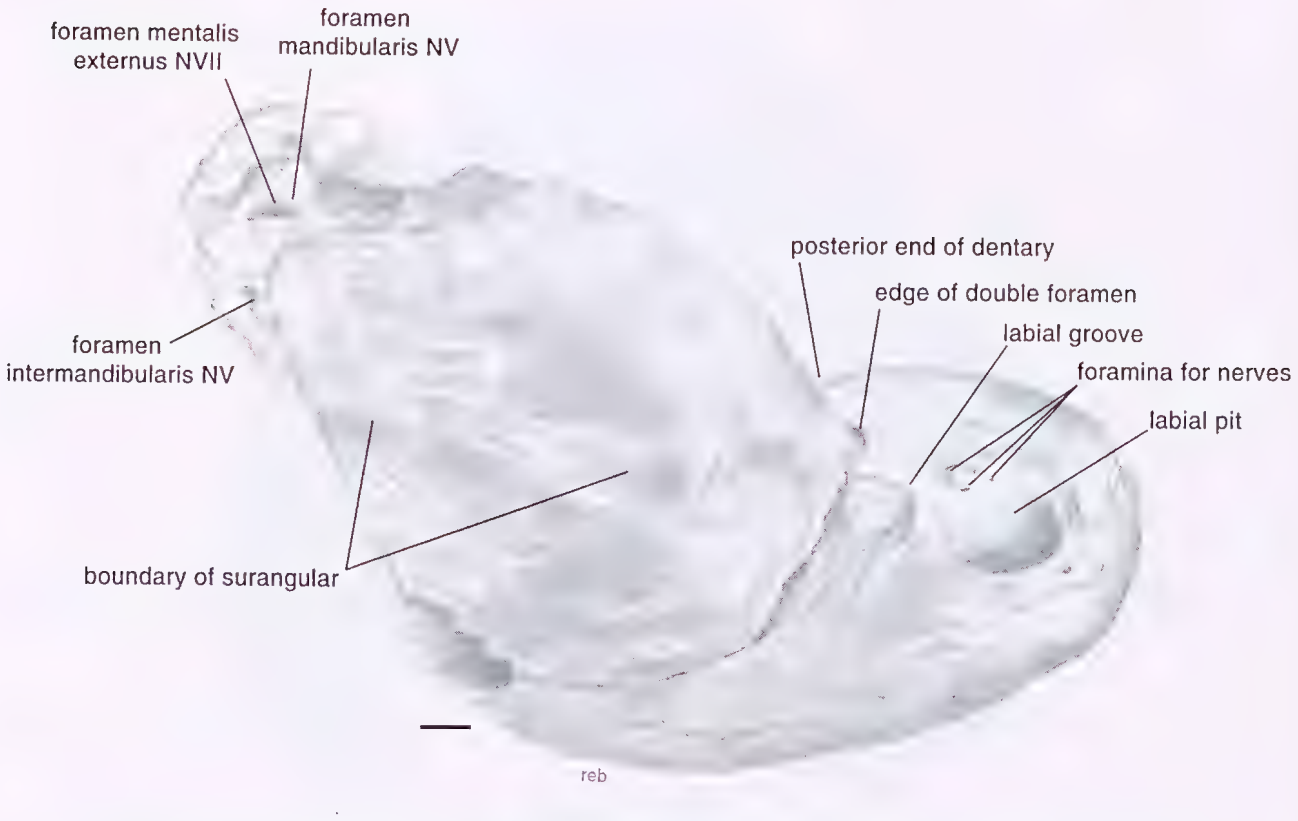

Figure 5. Right lateral view of the mandible of *Dipnorhynchus cathlesae*. The margin of the surangular is not clear and we have marked its ventral edge as "surangular" in its most probable position. Scales = 1 cm.

4. The **dental plate** (Figs. 3B, 4A, 7C) on the prearticular is up to 1.8 cm thick. It does not have any thick tubercles (or blisters; see White, 1966) such as occur in other dipnorhynchids. Surprisingly, this statement includes the large posterior tubercles (or blisters) as well as the anterior tubercles behind the anterior furrow. Is it possible that large tubercles were present originally, but have been removed by wear? Remaining on the surface are two or three low rounded longitudinal ridges, and a flattened median elevation behind the anterior furrow. In another work, we have shown that the eminences on the tooth plates in dipnorhynchids were formed by the addition of new tissue to the surfaces by upgrowth of new tissue on top of the underlying bones (Campbell & Barwick, in press), and in the discussion below, we discuss this matter further. Such eminences were modified by wear, but they were renewed on their surfaces by deposition from bony tubes through the underlying bone. Were the prearticulars smooth because of wear or because they were always without eminences? We have examined 12 mandibles of other dipnorhynchids, and on every one of them there is clear evidence of tubercles (blisters), even if they have been worn. Hence *D. cathlesae* is unique among dipnorhynchids in the structure of this part of its dental plate. Moreover the specimen has a distinct groove in the surface where other species have an anterior tubercle. So far as we are able to determine, this means that the dental surface was approximately flat, rather than tuberculate, throughout growth, and that the species crushed its food on a simple irregular grinding surface.

The margins of the prearticular against the adductor chamber consist of a sharp ridge without any sign of a rounded biting surface. Posteriorly this sharp ridge, formed by the junction of the dentine with the underlying bone, falls steeply into the posterior surface of the prearticular plate. The posterolateral surface adjacent to this dentine edge, makes a concave face medial to the glenoid fossa, and contains a wide open bony furrow which seems to have been floored, at least in part, by the articular laterally and the prearticular ventrally. The anterior part of this furrow has a broad shallow pit in which two or three nutrient openings are found (Fig. 6F). The posterior end of the structure is broken through, and clearly shows the coarse articular bone extending ventrally beneath the prearticular. Other well-preserved dipnorhynchids do not have a furrow in this position. On the contrary, the area is smooth, and passes posteriorly into the ridge on which was attached the pterygoid-mandibular ligament. Only the base of the pterygoid-mandibular ligament remains after breakage in *D. cathlesae*. The furrow described above must have been occupied by thick soft tissue forming the inner face of the glenoid fossa.

Although the glenoid fossa is not well preserved, it is known to be a posterodorsally directed opening, and is confined medially by a low bony ridge (Figs. 3B, 6F). Although the lateral and rotational movement of the mandible must have been controlled by the adductor muscles and a pterygoid-mandibular ligament, we also consider that the thick band of tissue in the position indicated would have served as a stabilising feature, confining the medial boundary of the glenoid fossa. The pressure on the

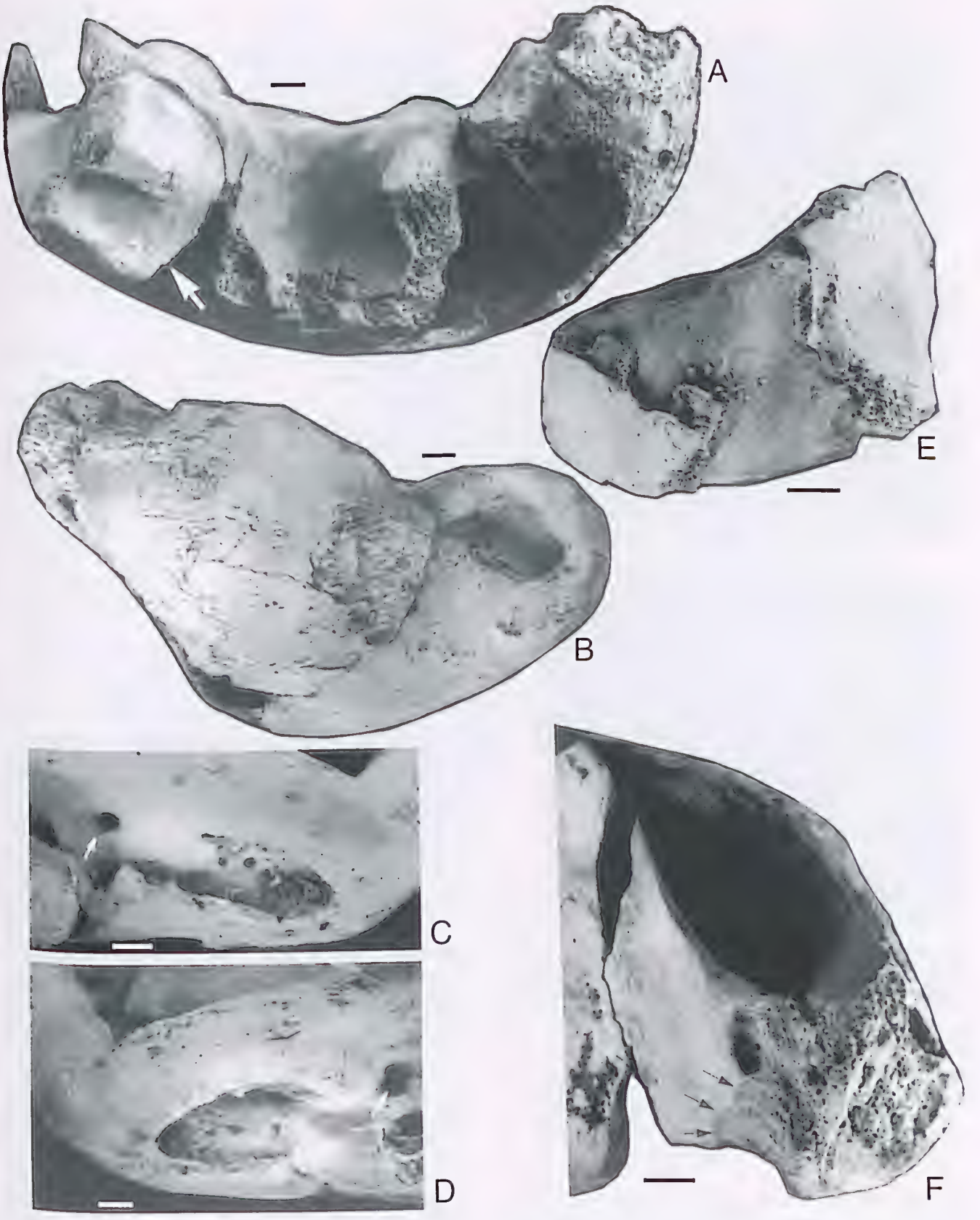

Figure 6. *Dipnorhynchus cathlesae*: A, posterior view; B, lateral view; C, D, dorsolateral views into the right and left labial pits. Note the foramina in the floors of the pits and the large foramina at their posterior ends, indicated by a white arrow in C and D. E, part of the mandible from the left side which was found down slope from the main specimen. Its position is shown by the large white arrow in Fig. 6A. Left side is external dermal bone; right side is the posterior face of the prearticular to the top left of the white arrow in Fig. 6A. Medial surface is where external bone was stripped off during preservation. F, right posterior end of the mandible showing the broken glenoid fossa, the sharp edge on the tooth-plate against the adductor fossa, and the sharp edged groove between the tooth-plate and the glenoid, marked by black arrows. Scales = 1 cm.

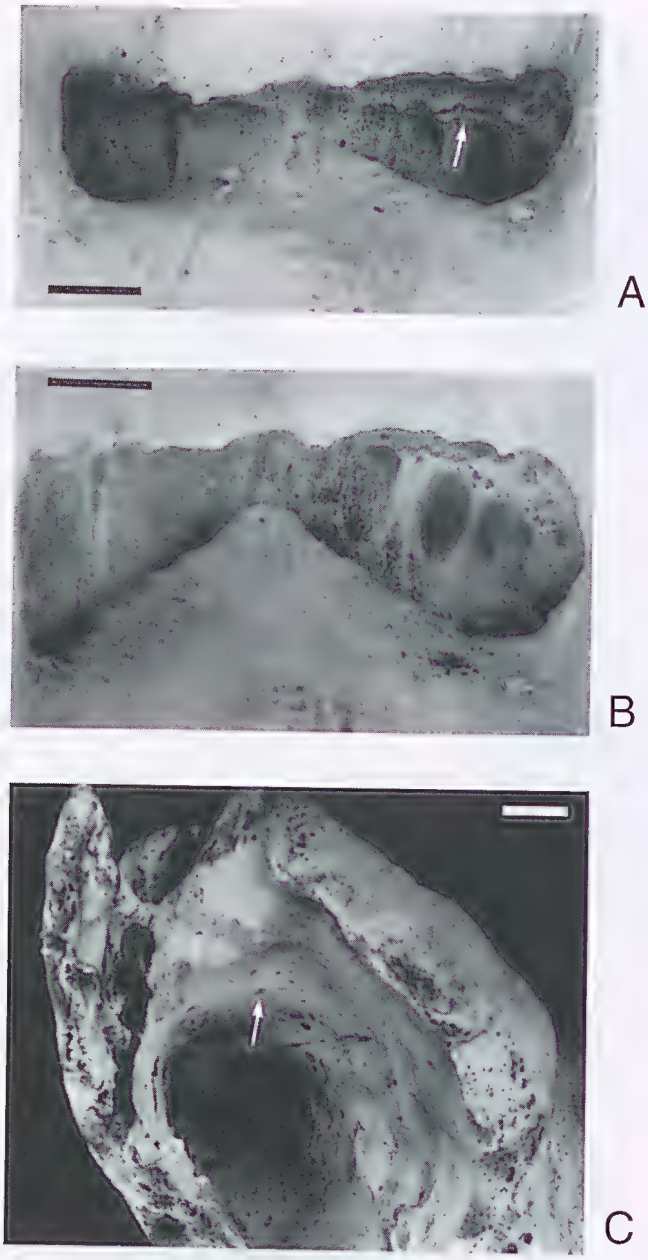

Figure 7. Two views into the anterior furrow of *Dipnorhynchus cathlesae*. A, with the specimen horizontal and B, with it tilted forwards. Note the abundance of pits on the right side and their scarcity on the left. The line of junction between the dentary and the endocranial bone shown by a white arrow. C, view down the adductor chamber on the left side of the specimen. The thickened prearticular is on the right. Note the ridges on the right wall, and the foramen (white arrow) with a short groove leading to the foramen at the posterior end of the labial pit. Many other nutrient foramina are also shown. Scales = 1 cm.

glenoid during a bite must have been very strong, and if large prey were being ground up on the dental plates, one would expect rotational forces to be periodically increased. Under these conditions; it is not surprising that extra support of the glenoid was developed.

The anterior end of the tooth plate is triangular in outline, but it does not rise up towards the dentary. On the contrary it declines perceptibly towards the anterior furrow, leaving behind it a gentle, rather flattened eminence. Against the anterior furrow, the tooth plate strongly overhangs the underlying endoskeletal bone.

We note that in *D. kurikae* the margins of the dental plate show signs of active growth and modification. In particular this applies to a small patch of the plate medial to the glenoid fossa, and along the posterior edge of the plate within and lateral to the lingual furrow. At these localities the continuous layer of dentine has a sharp margin, and patches of rounded or slightly elongate denticles occupy the surface. These indicate that the plate was growing at these points when death occurred. In *D. cathlesae* no denticles are present posterolaterally, but some are present within the lingual furrow along the edge of the plate.

5. **A section of the dental plate** (Figs. 11–14) cut near the posteromedial part of the plate, shows the arrangement of the tooth plate, the prearticular and the Meckelian bone. This section passes from the about the mid-length of the adductor opening to the lingual cavity, but it is sufficiently central to be considered as typical of the tooth plate. The specimen was studied in an optical section and from a surface cut parallel to this one and studied by SEM. The optical section clearly shows the presence of irregular canals that probably represent the sites of activity of micro-organisms, possibly fungal hyphae. Such features are known in other sections made from *Dipnorhynchus* specimens found at Wee Jasper and Taemas.

Deep weathering of the plate occurs along the medial side of the section, and along the dental surface, but fortunately some of this weathering is outside the main area of tooth-plate development. Peculiarities of the tooth plate have been recognised by workers on *Dipnorhynchus* since White (1966: 7) made the following comments: "the lower jaws of *Dipnorhynchus sussmilchi* ... do not shew tooth-plates with separate denticles but a crushing surface of raised blisters, large in extent but almost featureless, formed by a thickened layer of dentine continuous with the supporting bone." Clearly he thought that the material of the tooth-plate was dentine. The section accompanying that description (White, 1966: fig. 1) shows a cross section of the large rounded "blister" forming the posterior part of a tooth plate. The material referred to as "dentine" consists of long narrow tubes which extend to the surface of the tooth-plate, though some surface decomposition of the tissue took place before collection. No evidence of a basal pulp cavity is present. We have specimens of *D. kurikae* which show similar arrangements.

Naturally this kind of tooth-plate cannot grow in the same way as the plates of later dipnoans, because there is no addition of marginal teeth to permit lateral growth and no median suture to permit internal growth. Furthermore the blister-like tubercles on the plates of *D. sussmilchi* and *D. kurikae* increased their height and their palatal shape without being at the plate margin. Some of these blisters have a "botryoidal" appearance in oral view (Campbell & Barwick, 1985: figs. 8d, 9a) indicating that their buccal surfaces grew from several sites. In the absence of a pulp cavity, we must begin to be concerned that the material called "dentine" is not dentine of the kind as occurs in later dipnoans.

In *D. cathlesae*, the thin tubes of tissue forming the

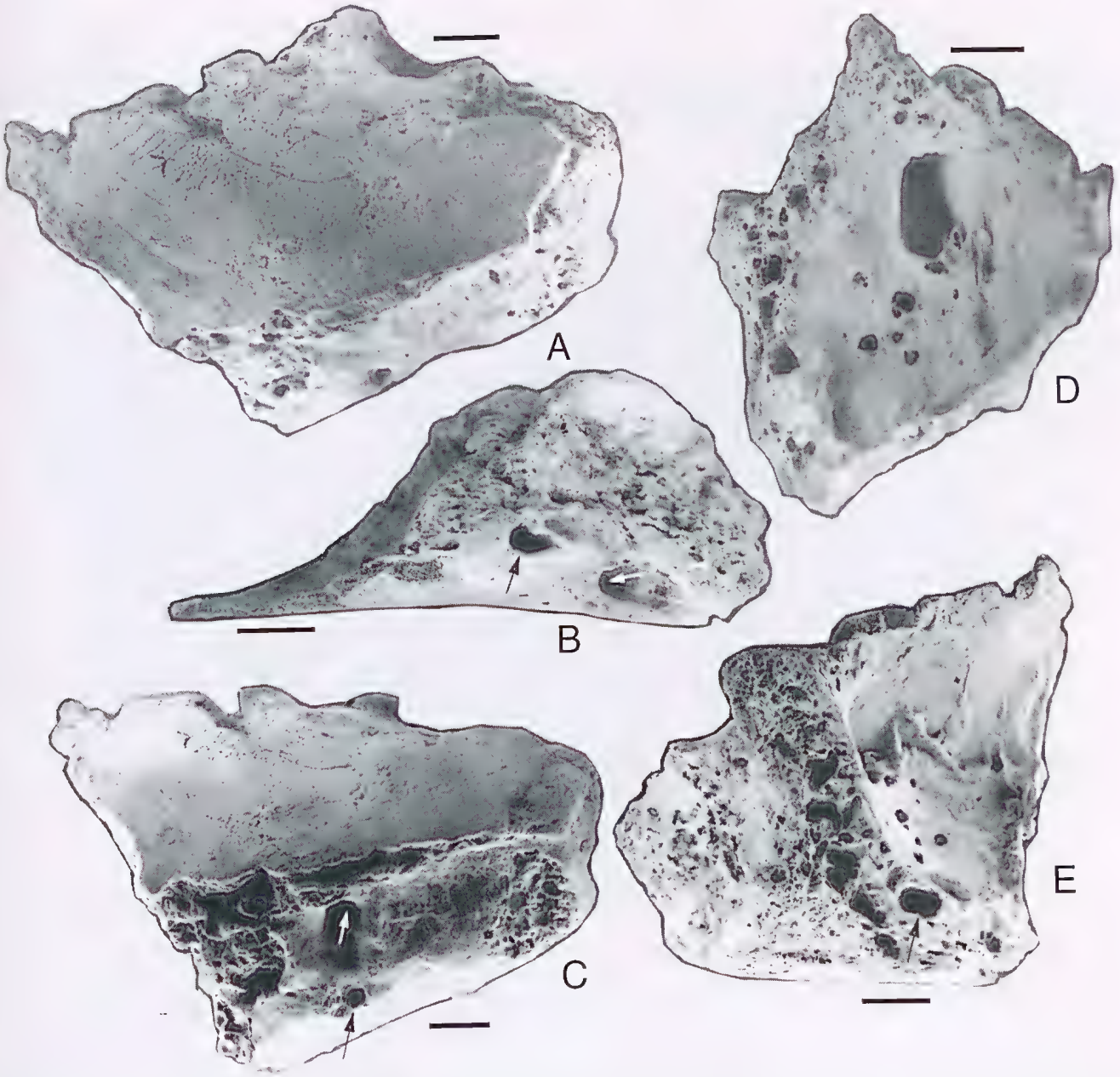

Figure 8. Views of the broken off fragment from the left corner of the specimen of *Dipnorhynchus cathlesae*. A, lateral view showing Westoll lines; B, dorsal view with the foramina for the ramus mandibularis V shown with a black arrow, and for the ramus mentalis externus VII shown with a white arrow; C, ventrolateral view showing the thick Meckelian bone with the large foramen for the ramus intermandibularis V shown with a white arrow, and a much smaller foramen for the ramus mentalis internus VII shown with a black arrow. The opposite end of the same canal is shown in E with a black arrow. D, E, two views of the internal surface showing the large foramen through which the nerves V and VII pass into the adductor chamber. Black arrow indicates the position of the ramus mentalis internus VII on the inner surface. Scales = 1 cm.

blisters have an irregular arrangement, but most of them are long and thin. A vertical section shows everything from longitudinal to transverse sections of the cavities. These cavities are filled with sediment, and some are branched. The walls are light coloured, but around the central canals is a darker layer. In several parts of the section, the hard tissue has strong concentric lines which indicates that recrystallisation has not taken place. These hard tissues should show dentine tubules, if the tubes are made of dentine, but in *D. cathlesae* no evidence of dentine tubules can be found, although it is clear that recrystallisation was **not** a factor in destroying fine structures. The absence of dentine tubules and the fact that reorganisation of the surface of the dental-plates took place merely by upward growth from preexisting bone, indicates that the tooth-plate grew by growth from the underlying bone. We deal with this problem in a publication on *D. kurikae* (Campbell & Barwick, in press).

The inner face of the prearticular is covered with bone of a different character. It is distinguished in thin section by layers of bone lying slightly oblique to the depositional surface, the layers being joined by short vertical struts. As shown on Figs. 11A,C, a thin layer without bone lies between this material and the prearticular. However, it is not continuous along the whole length of the section and it passes into lamellated bone at each end. We consider that

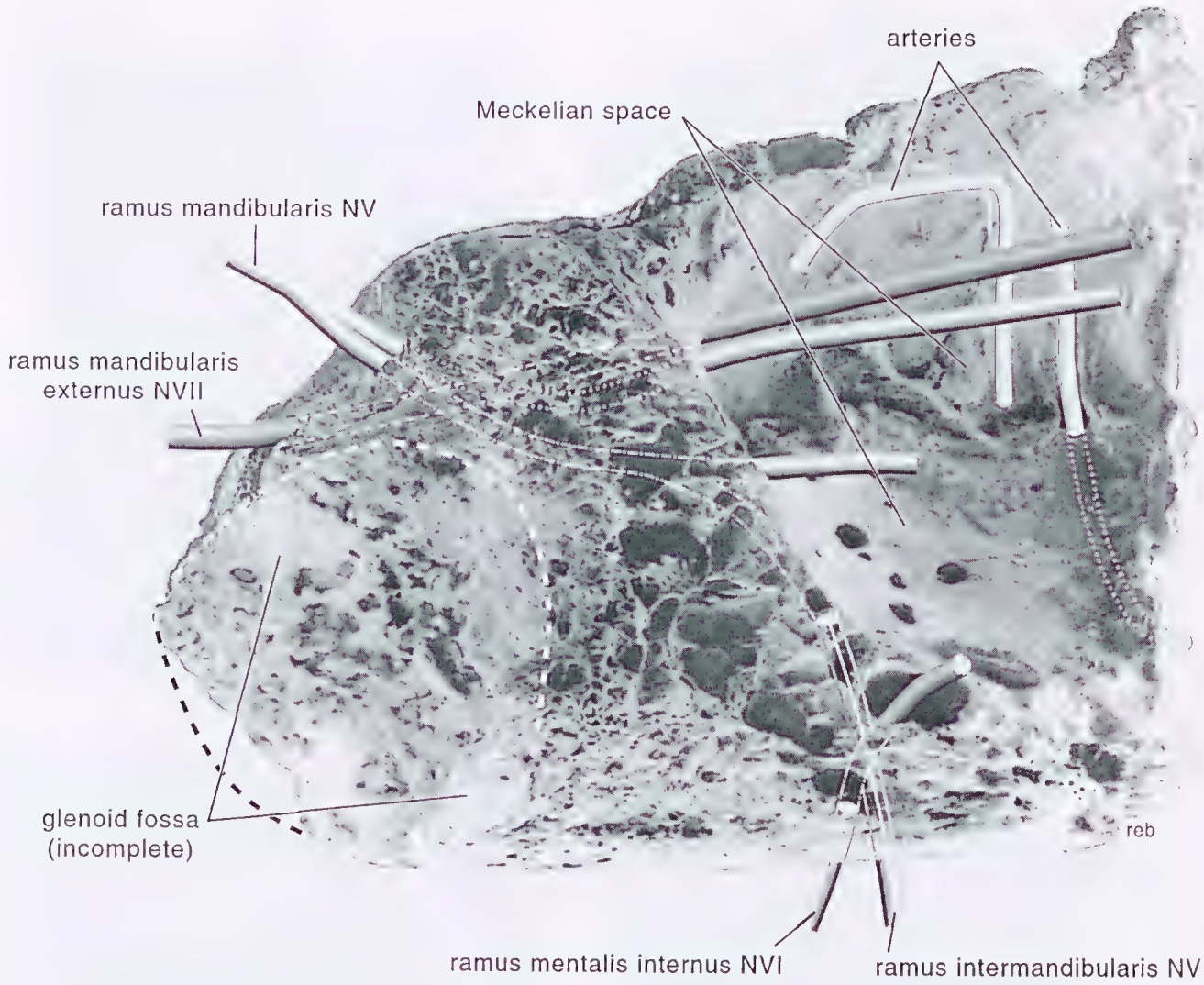

Figure 9. Reconstruction of the structures illustrated in Figs. 8D,E. Tubes buried in bone are indicated by broken lines. The glenoid is incomplete and is shown by a heavy dashed line. Two branches are shown for the ramus mandibularis nerve V whose paths are shown on the specimen. The internal branching of NV is well shown on the specimen. The arteries on the inner face of the surangular are shown by shallow grooves, and their paths are indicated.

the gap represents the sites of cells resorbing the Meckelian bone prior to deposition of new prearticular bone. The spaces between the bone layers are elongate. Optical sections show strong lines of growth parallel with the length of the lamellae, and these contain spaces which are also parallel with the lamellae (Figs. 11C, 12D, 14A). These are probably osteocyte spaces, and with the lamellar structure give an appearance which is quite different from that of the bone spaces in the prearticular bone. Is this bone a precursor of the prearticular, or is it a lining of Meckelian bone which occurs around the adductor chamber in other dipnoans? We know of no instance where a precursor of a dermal bone was laid down in bone which is so different in bone so different from the dermal bone itself. Observation of the interior of the adductor chamber shows that the layer runs forwards and around onto the external bone in the normal way that Meckelian bone does. Hence this seems the most appropriate name for the bone.

Between the thin-layered Meckelian bone and the main bone of the prearticular, there is a linear series of bone layers more widely separated than those in the Meckelian bone (Figs. 11A,C). These lines of bones are gradually disappear laterally towards the inner edge above the posterior face of the mandible. The separation of bony layers is greater than in the Meckelian layers, and the openings between the layers is more elongate and thicker. These inner layers give the appearance of older Meckelian bone layers which have been partly modified by later activity of bone deposition. We note also that these lamellae have a similar internal structure to the main Meckelian bone, and it is easily distinguished from the intergrown porous bone which invades it.

Meckelian bone was thickened along the surface bordering the adductor chamber as would be expected. The prearticular thickens by resorption of the inner surface of the Meckelian bone and replacement by vascular bone of the usual prearticular type. This is seen particularly well on Fig. 11C. The thickness and the laminated texture of the Meckelian bone are possibly to be explained by the magnitude of the adductor muscles which were attached to it.

This interpretation is supported by our observations on the specimens of *Chirodipterus australis* and *Holodipterus gogoensis* etched from the Gogo faunas. In those species

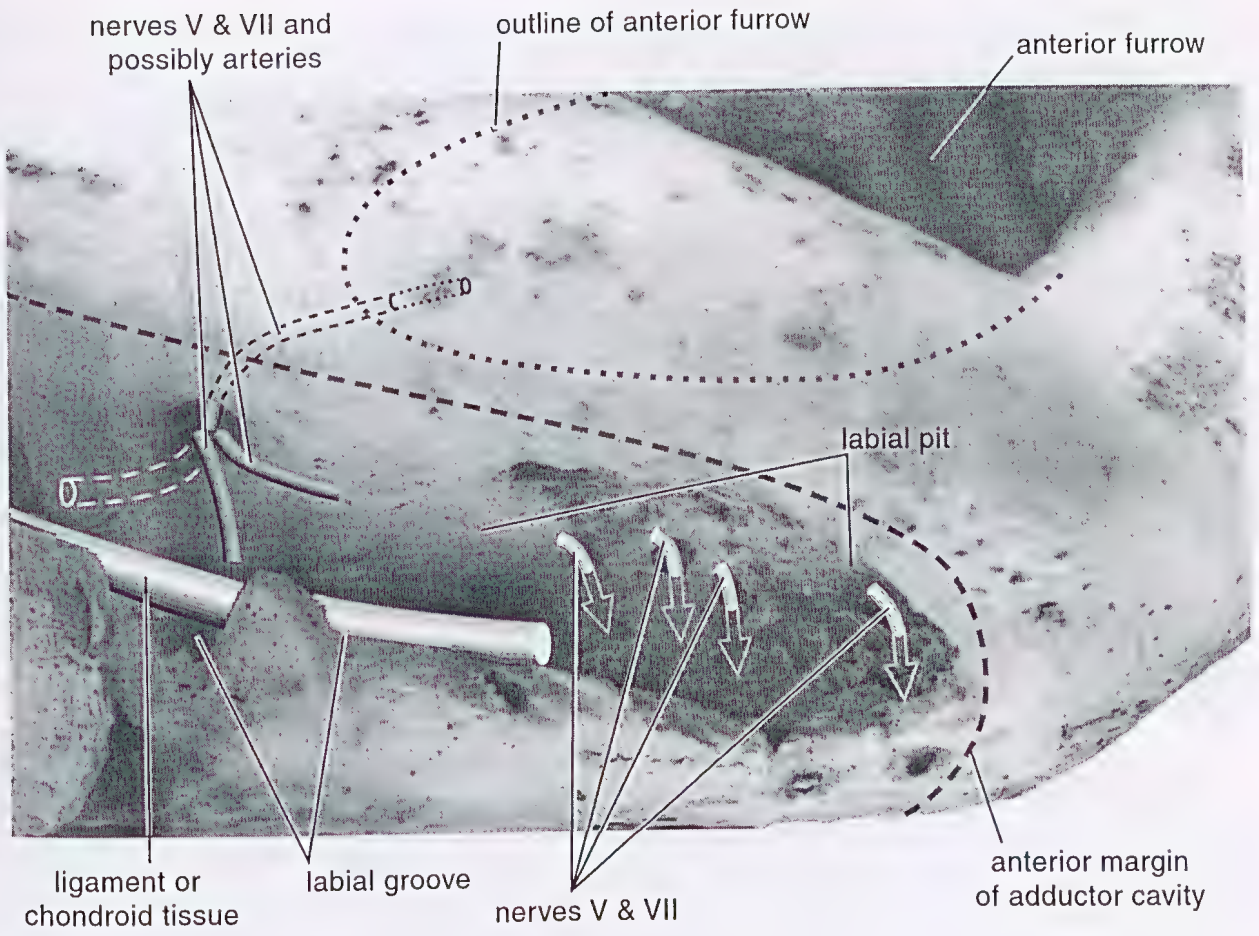

Figure 10. Reconstruction of the right labial pit showing the passage of the ligament or the chondroid tissue from the adductor chamber to the labial pit; some of the nerves V and VII running from the adductor cavity to the labial pit; and the nerves V and VII running through the large foramen at the posterior end of the labial pit and also into the anterior furrow. Parts of the canals buried in the bone are shown with a linear symbol or with a dotted margins.

much of the adductor space is lined by a thin layer of Meckelian bone which continues anteriorly from the articular bone. A gap is left between the prearticular and the inner lining of the Meckelian bone, and this must have been filled by the Meckelian cartilage. The prearticular was able to expand inwards by occupying this space and replacing the cartilage. The thin lining of the bone around the adductor chamber must have been resorbed and redeposited during growth. In *D. cathlesae*, no space was left to be occupied by the Meckelian cartilage. The Meckelian bone against the adductor chamber was much thicker than in the other two species, and continued to grow inwards as the prearticular expanded into the space previously occupied by Meckelian bone. This arrangement is interesting because it confirms the view that little growth took place on the buccal layers of the prearticular, and hence the absence of tubercles (blisters) on the grinding surfaces. Most of the thickening of the prearticulars took place by the rapid inward growth, occupying space originally occupied by Meckelian bone.

6. The **glenoid fossa** (Figs. 3B, 4A, 6F, 9) is not well exposed on either side of the specimen, but parts of both the articular bones remain. We have recently discovered that in *D. kurikae*, the preglenoid process has a strong dorsally directed ligament attachment on its dorsal surface immediately inside the surangular. In *D. cathlesae* the surface of the articular in front of the glenoid fossa is flattened, and could have provided a surface for the attachment of a ligament. This surface is not extended forwards as a process plastered on the inner surface of the surangular on which ligaments could be attached, a feature found in other dipnorhynchids (Campbell & Barwick, 1985: figs. 8a, 9). Such a structure is exposed to weathering, and it could have been removed before collection of *D. cathlesae*. However, even if such a structure was not present, the articulation of the jaw would have been supported by the connective tissue forming the inner face of the glenoid region as shown in section 4 above. The matter will be further discussed in our paper on *D. kurikae*.

7. In dorsal view, the **adductor opening or fossa** (Figs. 3B, 4A, 6F) is pear shaped, being much wider posteriorly. Two cm from its posterior edge, it measures 4 cm across from crest to crest, and narrows gradually in front of that. This is a very different shape from the more parallel sided adductor opening in *D. kurikae*, in which the opening narrows down only within a short distance of the anterior end. In *D. cathlesae*, the lower medial wall of the adductor chamber formed by the inner face of the prearticular, is

very roughly ridged (Fig. 7C), almost to the anterior edge of the chamber. The coarse vertical ridges on the inner wall of the chamber extends much further forward than one would expect, reaching well up under the anterior furrow. Both sides of the specimen, but particularly the left, also have a few anteriorly directed ridges on the inner face of the outer wall of the chamber. On *D. kurikae* the ridging is not so powerful and does not extend so far up the inner face of the chamber. In *D. cathlesae* the adductor muscles were very strong and some of them were attached far forward of the anterior margin of the adductor opening, and on inner and outer sides of the adductor chamber.

In *D. kurikae*, the articular runs forwards along the edge of the prearticular on the upper edge of the adductor opening, making a distinct rounded ridge which shows so well in dorsal view. In *D. cathlesae*, the articular is present in this position, but it does not appear as a rounded ridge in dorsal view (Figs. 3B, 4A). The reason for this is that the prearticular rises high against the edge of the adductor chamber, and the articular is smoothed out against it rather than forming a rounded ridge. This feature is obviously related to the way in which the tooth plate comes to a crest along its lateral margin.

8. The **lingual furrow** (Figs. 4A,B) is slight, has an almost vertical lower face ventrally on the prearticulars, but turns over into a shallow groove dorsally. The lower vertical part is very high as compared with that of *D. kurikae*. The prearticulars forming the lateral parts of the front wall of the lingual cavity are thick, and they are deeply concave, overhung by a projection on the tooth plates.

The anterior space for the tongue is short and narrow, though the posterior part must have been wide. In the posterior face of the prearticular bone is a broad deep cavity into which the lateral parts of the tongue pad would have fitted. Judging from the position in extant dipnoans, the anterior part of the tongue would have been short, and would not have extended forwards into the space occupied ventrally by the rounded eminence in the median floor. The whole contour of this region indicates that the hyoid system would have been very posterior in position and would have had little opportunity to move dorsally and ventrally to control the buccal space. This emphasizes emphatically that the hyoid arch would not have been able to compress an air space in the back of the buccal cavity as would have been required for air breathing along the same lines as in extant dipnoans.

At their ventral edge on the posterior face of the mandible, where the prearticulars join the dermal bones, the prearticulars have a distinctive inturning towards the dermal bone. This leaves a flange around the specimen which is larger than any other species of the genus.

9. The **nerve canals** (Figs. 3B, 4A,B, 8, 9) lateral to the glenoid fossa are quite different on the two sides of the specimen. On the left, two large foramina lie between the articular and the surangular. The more posterior one is more laterally placed and passes posterodorsally into a deep groove which runs off the articular. It presumably contained a branch of the nerve ramus mentalis externus VII (*f me VII* of Thomson & Campbell, 1971). Note that Miles (1977: fig. 102) has two branches of this nerve in *Chirodipterus australis*, but he was unsure about the significance of this because the two did not appear in all specimens. Internally this large foramen in *D. cathlesae* opened after a short course into a large chamber. Within this chamber the courses of the furrows are not clear, but the VIIth nerve enters a groove which ran down the inner face of the surangular bone. The dorsal one is small and lies at the top of the foramen and cannot be traced anteriorly. The lateral one lies against the surangular and continues along the inner face of that bone.

The more anterior foramen on the left side of the dorsal surface of the bone is of about the same size as the posterior one, but it passes through the articular in a more dorsomedial orientation than the ramus mentalis externus (*f me VII* of Thomson & Campbell, 1971), into the same large internal chamber. On the external surface this groove seems to be entered by two foramina, the anterior one being dorsally and the lateral one being posterodorsally directed. Its position in the chamber and anterior to it is not clear on the specimen, but it sends a groove down the inner face of the chamber to run to the foramen intermandibularis V (see below) on the ventral surface of the mandible. The anterior opening of the chamber shows a rounded edge indicating that a branch of nerve V passed into the adductor chamber away from its walls, and hence into the adductor muscles. Up towards the dorsal foramen, another branch joins the groove that carries the ramus VII forwards along the surangular. We consider that it carried the mandibularis V along with the mandibularis VII to the anterior end of the mandible.

Opening ventrally out of the mandible is a large rounded foramen in the articular, rather than at the junction between the dermal bone and the articular. It would have transmitted the intermandibularis nerve V (*f int V* of Thomson & Campbell, 1971). In addition to the V nerve, we expect from the above description that it also contained branches of the VII nerve. As would have been expected, the grooves leave this foramen in anterior, ventral and posterior directions innervating the elongate intermandibularis muscle.

Ventral to this foramen for the ramus intermandibularis V nerve (*f int V* of Thomson & Campbell, 1971) is a much smaller foramen which connects through the articular below the floor of the adductor chamber in a much larger foramen on the broken internal surface. The right side of the specimen apparently had a similar structure, but it has been broken through during preservation. A similar foramen has been recorded by Miles (1977) in *Chirodipterus* which he labelled *cr.c*, and he indicated only that it was the "posterior cross canal". He did not indicate the function of this structure. Because of its position and the presence of small openings in its wall making connections with the surrounding bone, we consider that this system contained a nerve. The canal is in an appropriate position for the ramus mentalis internus VII nerve, according to the reconstructions of *Neoceratodus* by Fox (1965).

Miles (1977: 204) commented that he considered the mandibularis V nerve to have passed through the adductor fossa, and that "all the openings in this region, in both *Dipnorhynchus* and *Chirodipterus* transmitted branches of the *R. mentalis externus VII*". Our specimen shows that the nerve V would not have passed in this way; indeed some of our specimens of *C. australis* indicate the same point. It

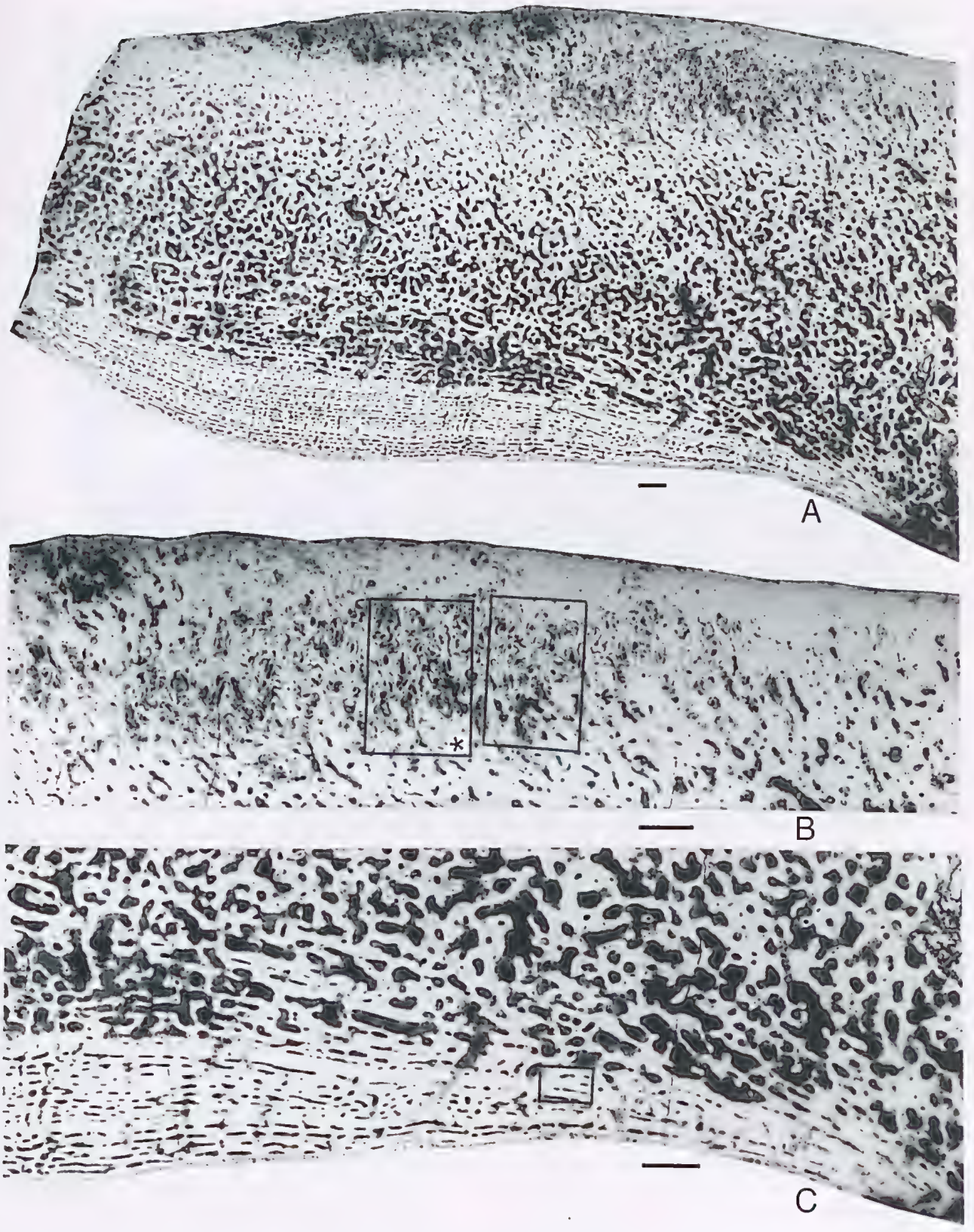

Figure 11. Sections of the prearticular of *Dipnorhynchus cathlesae*. A, transverse section as shown by the black arrow on Fig. 3B. The left side is towards the adductor fossa, and the right onto the posterior wall of the mandible. A thin layer of sediment is left attached to the base of the section. A, shows the Meckelian bone at the base overlain by thin layers of Meckelian bone being transformed into prearticular bone. At the top is a change in texture where the prearticular is replaced by so-called "dentine". The boundary between the two tissues is marked by discontinuities. The topmost part of the section is so weathered that no detail can be seen in it. B, enlargement of the top of A showing the contact between the main bone of the prearticular and the so-called "dentine". The uppermost surface is weathered. C, enlarged part of the Meckelian bone and contact with the prearticular. Note how the layers in the laminae change abruptly to become less continuous in the prearticular. Scales = 1 mm.

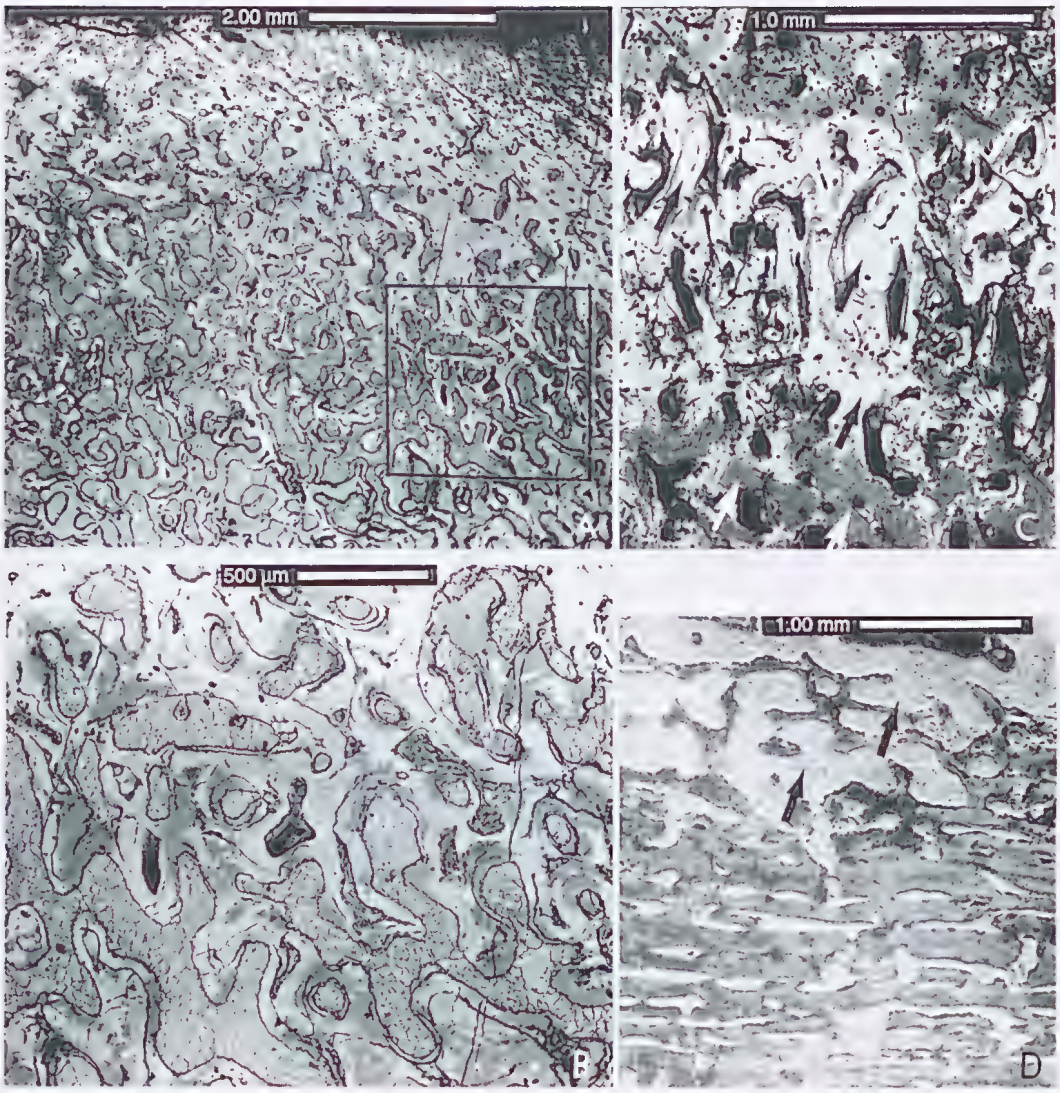

Figure 12. A–C, back scattered SEM figures taken from a slice cut parallel with the section in Fig. 11. A, shows the transition between the dark coloured bone at the base and the lighter coloured so-called "dentine" at the top. B, enlargement of the area shown on A. Note the absence of any continuous gap between the two types of tissue. The crazed pattern is calcite infilling the specimen. C, specimen of the tissue near the top of the section showing the elongate spaces in the so-called "dentine" (black arrow), and the bone at the base (white arrows). D, section through the Meckelian bone showing lamination and the abundance of elongate osteocyte spaces. Note the transition from the closely layered Meckelian bone at the base into the overlying bone. Black arrows indicate calcite infillings of the matrix.

will be obvious that we consider the complication suggested by Miles to be unnecessary, and that Thomson & Campbell (1971) were correct in having both nerves V and VII oriented as they suggested.

On the right posterodorsal side of *D. cathlesae*, there is a single opening which is larger than either of the nerve openings on the left side of the specimen. The inner wall of this opening has a ridge which separated the two nerves entering the foramen. The posterior opening is by far the smaller one and the more dorsal opening is almost vertical. We consider that these are for the ramus mentalis externus VII and the ramus mandibularis V respectively. The internal cavity within the articular is smaller than the one on the other side, and its anterior opening is also smaller.

10. The **infradentary bones** (Figs. 3A, 5, 6B) are moderately well exposed, especially on the right side of the specimen. They were originally covered with cosmine, but wear has removed some of that tissue. On the right side the posterior part of the surangular is exposed. It has an acute posterior end which rises high on the side of the mandible and lies immediately beneath the foramen for the ramus mentalis externus VII. This is unusually high in comparison with *D. kurikae* and *D. sussmilchi*, in which a granulated surface occupies the upper part of the bone.

Westoll lines are obvious on the surangular on the left side (Figs. 8A,C). They close posteriorly where they turn upwards slightly to produce a banana shape. The ventral edge of the surangular is exposed incompletely on the right side of the specimen, and gives the impression that the bone runs forward to the ventral edge of the labial pit, though its anterior edge cannot be seen. This is appropriate for a dipnorhynchid, in which the surangular is always long. On the right side the lateral line canal is visible lying about half way down the bone.

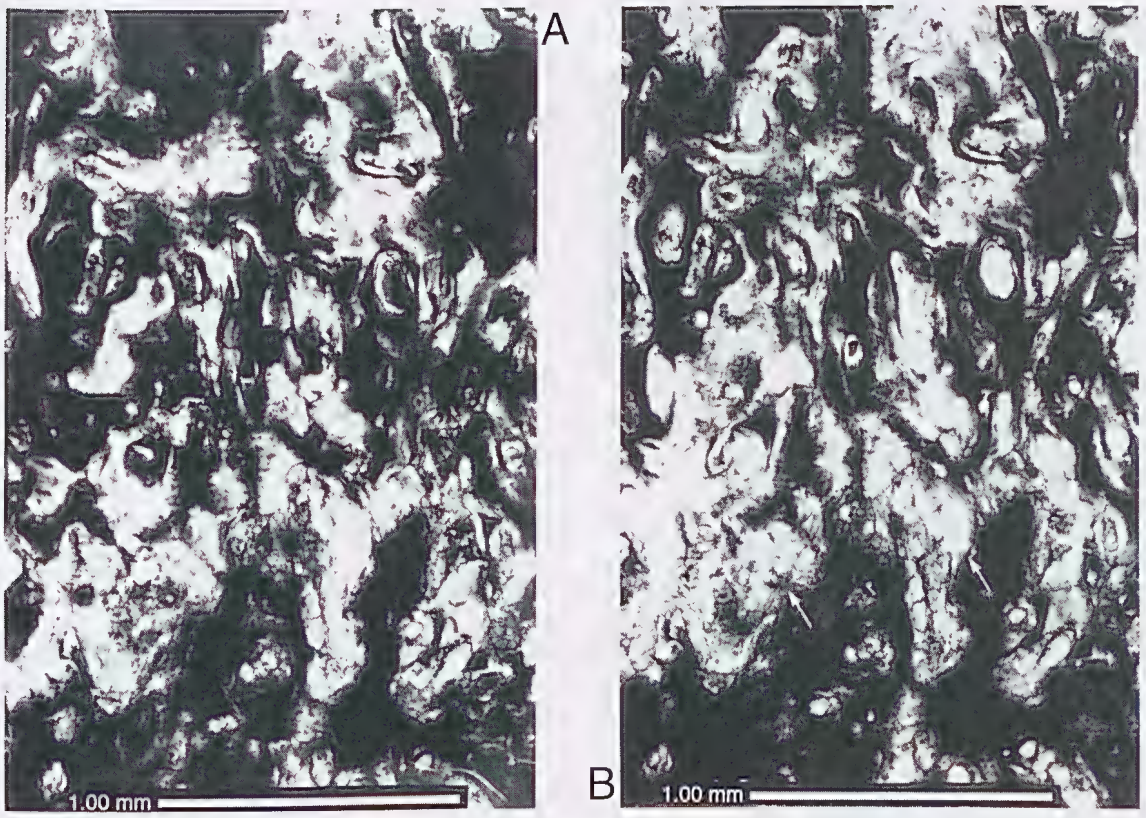

Figure 13. Two views of the one position of the optical section outlined in Fig. 11B marked with an asterisk. A, crossed polarised light and B, single polarised light. At the base the tissue is prearticular bone, and at the top it is the so-called "dentine". The large areas marked with the white arrows are infillings of the open spaces between the bone and the so-called "dentine".

11. Because the **posterior edges of the infradentaries** (Fig. 6A) are badly worn, it is not possible to give precise positions for all the foramina which usually occur along the line between the infradentaries on the one hand, and the prearticulars and the Meckelian bone on the other. In *D. kurikae*, the largest foramen along this line is figured by Campbell & Barwick (1985: fig. 8B), but it was unlabelled. Several other topotypes of *D. kurikae* have since become available, and all show this feature. *Dipnorhynchus sussmilchi* has a smaller foramen in this position, and one or two other foramina medial to it. The specimen of *D. cathlesae* is poorly preserved in this region on both sides of the specimen, but on the left side the broken surface shows a large foramen passing between the Meckelian bone and the infradentaries. It is a section across a canal which continues forward and enters the adductor chamber in a forwards position. This is in the same position as the foramen in *D. kurikae*, and the foramen for the efferent branchial artery in *D. sussmilchi* (Thomson & Campbell, 1971: fig. 22).

Specimens of *D. sussmilchi* show strong canals on the face of the prearticular in the adductor chamber (Thomson & Campbell, 1971: figs. 47–49). These develop from a foramen which lies between the postsplenial and the prearticular. A similar groove is found in *D. cathlesae* running up the surface through the bone forming the coarse ridges used for muscle attachment, then across the under surface of of the dental plate and then into a fossa in the plate at the level of the anterior end of the adductor fossa. It enters a deep tube in the plate, and can be traced through the plate in an anterior direction, emerging in the posterior corner of the anterior pit. Further back along this main canal where a sharp turn forwards occurs, a weaker canal runs forward along the line indicated by the symbol *sa1* by Thomson & Campbell (1971: fig. 22). The more posterior branch of the canal running to f_1 *sa 1* in *D. sussmilchi* is not well represented on our specimen, mainly because the specimen is poorly preserved in that region.

We point out that the canals as in *D. sussmilchi* have now been found in new specimens of *D. kurikae* and in *D. cathlesae*. No matter how we interpret these structures in functional terms, it is clear that they are features found in all dipnorhynchids.

Comparisons

In the above description we have concentrated on comparisons with *D. kurikae*, which is the species stratigraphically closest to *D. cathlesae*, and also occurs in the Wee Jasper sequence. The only other species in which the mandible is known is *D. sussmilchi*, the type species. This was described by Thomson & Campbell (1971). Since that time we have discovered three imperfect specimens of *D. sussmilchi* in the *Spinella yassensis* Limestone, some of which allow us to add to the previous description.

In *D. sussmilchi* the lingual furrow is deeper and proportionately narrower than that of *D. kurikae*. It continues forward as a distinct furrow to the anterior furrow which lies just medial to and slightly behind the end of the

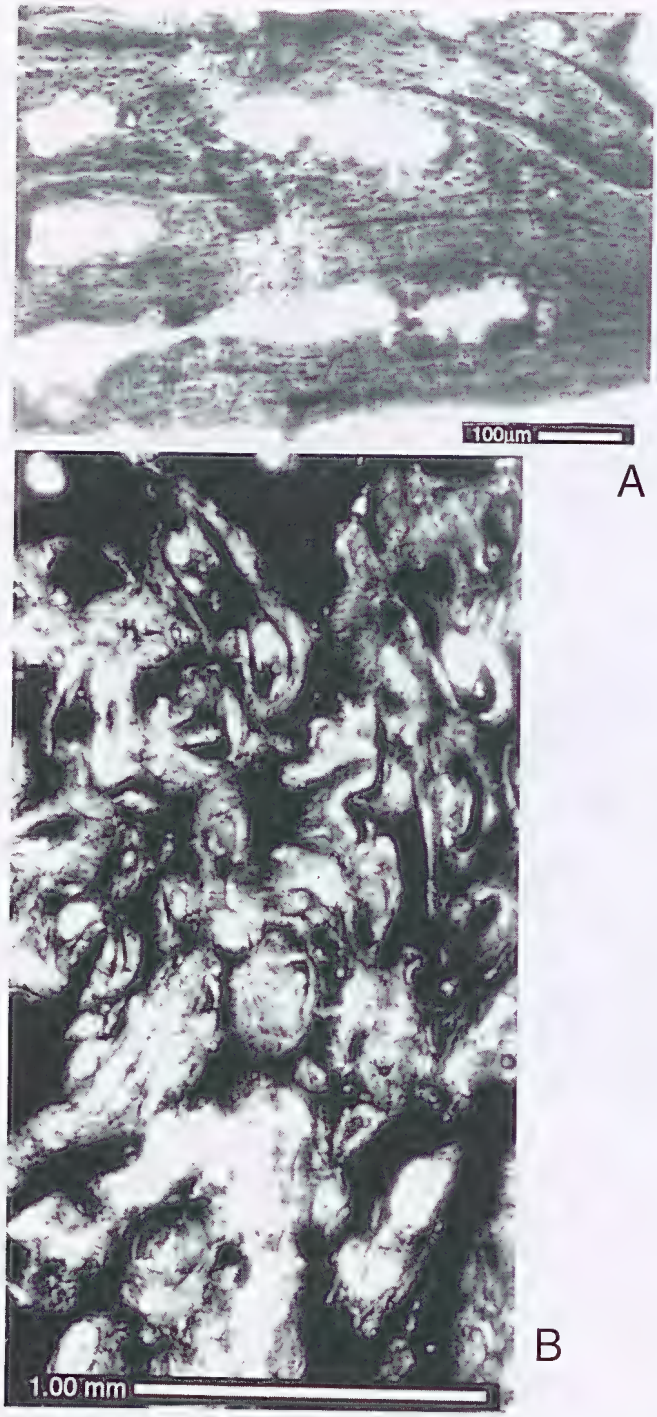

Figure 14. A, enlarged part of the Meckelian bone (outlined on Fig. 11C). It shows the lamination and the abundant osteocyte spaces. B, section under crossed polars. Its position is the right rectangle shown on Fig. 11B. It crosses the boundary between the prearticular bone at the base and the so-called "dentine" at the top. The two images are reversed in comparison with Fig. 11.

anterior furrow. Posterior to this is a deep groove, the inner edge of which is well defined by a ridge that extends back to the large rounded posterior protuberance forming the main grinding face of the tooth plate. In all these features, *D. sussmilchi* is unlike *D. kurikae*, and even less like *D. cathlesae*. Like *D. kurikae*, *D. sussmilchi* has a similar groove running between the lateral margin of the tooth plate and the posterior protuberance. We have also noticed that the articular has a projection in front of the glenoid fossa to which was attached a muscle as in *D. kurikae*. This is not present to anything like the same extent on *D. cathlesae*. Finally, the lip pit on *D. sussmilchi* has a well-rounded anterior edge and does not extend into a furrow as in the other species.

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Monophyly, Interrelationships and Description of Three New Genera in the Dottyback Fish Subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae)

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ABSTRACT. Within the Pseudochromidae, the subfamily Pseudoplesiopinae is diagnosed by six unequivocal autapomorphies: single tubed lateral-line scale; posterior part of pelvic bone with triangular or hook-shaped lateral process; base of anterior process on pelvic bone posteriorly positioned; coracoid articulates ventrally with medial face of lateral lamina of cleithrum; basihyal bound to anterior face of basibranchial 1; and urohyal with prominent dorsally directed process. Five genera are recognised in the subfamily. *Pseudoplesiops* Bleeker (*Nematochromis* Weber is a junior synonym), with seven nominal species, is diagnosed by a single autapomorphy: medial laminae of pelvic bones expanded dorsally. *Chlidichthys* Smith (*Wamizichthys* Smith is a junior synonym), with 10 nominal species, is diagnosed by two autapomorphies: lower lip incomplete; and second infraorbital bone absent. *Pectinochromis* n.gen. (type species *Pseudoplesiops lubbocki* Edwards & Randall), with a single nominal species, is diagnosed by five autapomorphies: second dorsal-fin pterygiophore inserting between neural spine 3 and 4; second supraneural bone absent; first dorsal-fin pterygiophore expanded anteriorly; first dorsal-fin pterygiophore with lateral processes; and gill rakers relatively numerous. *Amsichthys* n.gen. (type species *Pseudoplesiops knighti* Allen), with a single nominal species, is diagnosed by a single autapomorphy: upper preopercular pore usually absent. *Lubbockichthys* n.gen. (type species *Pseudoplesiops multisquamatus* Allen), with a single nominal species, is diagnosed by four autapomorphies: scales small; scales cycloid at all stages of ontogeny; some head bones with weakly honeycombed surface; and parietal enclosing dorsal part of supratemporal laterosensory canal. A parsimony analysis of various characters of the laterosensory system, caudal skeleton, dorsal-fin osteology, and fin-ray branching supports the following relationships: (*Lubbockichthys* ((*Amsichthys* + *Pseudoplesiops*) (*Chlidichthys* + *Pectinochromis*))).

GILL, ANTHONY C., & ALASDAIR J. EDWARDS, 1999. Monophyly, interrelationships and description of three new genera in the dottyback fish subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae). *Records of the Australian Museum* 51(2): 141–160.

The Pseudochromidae is a family of small, reef-associated fishes, which are distributed throughout the Indo-Pacific. The family is currently divided into four subfamilies: Anisochrominae, Congrogadinae, Pseudochrominae and Pseudoplesiopinae (Godkin & Winterbottom, 1985). The objectives of the present paper are to provide evidence for monophyly of the Pseudoplesiopinae, to diagnose its included genera, and to investigate phylogenetic relationships among those genera. Species-level revisions of the genera will be provided in forthcoming papers by the present authors.

Historical review of the systematics of the Pseudoplesiopinae

Bleeker (1858) described the genus *Pseudoplesiops* for a new species, *P. typus*, from a single specimen from Goram (= Manawoka), Indonesia. He assigned it to his family Pseudochromides [sic], noting that it fell between *Pseudochromis* Rüppell and *Plesiops* Oken (now Plesiopidae) in morphology. He described it as having: dorsal fin with 16 unbranched and nine or 10 branched rays; anal fin with seven unbranched and nine branched rays; pelvic fin with no spine and five rays, the outer two elongate and filiform; palatine teeth absent; scales cycloid; and a single anterodorsal lateral line consisting of inconspicuously pored scales. He later (Bleeker, 1875) reported on an additional specimen of the species from Ambon (actually referable to a new *Pseudoplesiops* species, which we will describe elsewhere) and included the species as sole member of the Pseudoplesiopini, one of three groupings he recognised within his family "Pseudochromidoïdes." The remaining two groupings were Cichlopini, for *Cichlops* Müller & Troschel (= *Labracinus* Schlegel), *Pseudochromis* Rüppell, *Pseudogramma* Bleeker (now in Serranidae), *Gramma* Poey (now in Grammatidae) and *Trachinops* Günther (now in Plesiopidae), and Plesiopini for *Plesiops* Oken and *Paraplesiops* Bleeker (both now in Plesiopidae).

Günther (1860) assigned *Pseudoplesiops* to his Pseudochromides, which he treated as a subgroup of the Trachinidae, along with *Pseudochromis, Cichlops, Opisthognathus* [sic] Cuvier (now Opistognathidae), *Notothenia* Richardson (now Nototheniidae), *Harpagifer* Richardson (now Harpagiferidae), *Heterostichus* Girard (now Clinidae) and *Pegetodes* Richardson (now Channichthyidae).

Boulenger (1895: 336) listed *Pseudoplesiops* in the Serranidae and noted that it "appears to combine characters of *Callanthias* [now in Callanthiidae] and *Plesiops*." Boulenger did not comment on the position of *Pseudochromis* and *Cichlops* in this paper, but later (Boulenger, 1901) placed them and genera now assigned to the Opistognathidae, Malacanthidae and Bathymasteridae in the Pseudochromidae.

Boulenger (1899) apparently overlooked Bleeker's (1858) use of *Pseudoplesiops* (despite his own 1895 reference to *Pseudoplesiops* Bleeker) and described *Pseudoplesiops* as a new genus for a new species of cichlid from the Congo, *P. nudiceps*. He later (1902) described another new species in the genus from the Congo, *P. squamiceps*. Pellegrin (1904) noted that *Pseudoplesiops* Boulenger was preoccupied and proposed a replacement name, *Nanochromis* (often subsequently misspelt *Nannochromis*).

Regan (1913) classified *Pseudoplesiops* in its own family, Pseudoplesiopidae, but included *Pseudochromis* and *Cichlops* in the Serranidae.

Weber (1913) described a new genus and species, *Nematochromis annae*, from two syntypes collected in Indonesia during the Siboga Expedition, one from Sarasa Island, Postilon Islands, and the other from Solor Strait. He described the species as having: dorsal and anal fins with two weak spines and mostly undivided, segmented rays, totalling 26–27 and 15 rays, respectively; pelvic fin with a weak spine and three unbranched, segmented rays; and lateral line interrupted, consisting of an anterodorsal series of 30 grooved scales and a midlateral posterior series of 15 grooved scales. He assigned the species to the Pseudochromidae.

Jordan (1923) provided a classification for nominal fish genera. He included only *Pseudoplesiops* in the Pseudoplesiopidae, retaining *Nematochromis* in the Pseudochromidae.

Weber & de Beaufort (1929) reexamined the holotype of *Pseudoplesiops typus* and modified some of the characters given by Bleeker (1858). Most notably, they reported in the generic diagnosis that the pelvic fin had I,4 rays, the first segmented ray thickened, produced and bifid, but reported in the species diagnosis that all segmented rays are simple, and that the anterior two are thickened and elongate. Weber & de Beaufort (1929, 1931) generally followed Regan's (1913) classification, but recognised the Pseudochromidinae [sic] as a serranid subfamily containing *Nematochromis, Dampieria* Castelnau (= *Labracinus*), *Pseudochromis* and *Pseudogramma*.

Berg (1940) also followed Regan's assignment of *Pseudoplesiops* to its own family, while retaining "pseudochromids" in the Serranidae.

Fowler (1931) recognised three subfamilies within the Pseudochrominae: Pseudogramminae (*Pseudogramma*); Pseudochrominae (*Dampieria, Pseudochromis* and *Nematochromis*); and Pseudoplesiopsinae [sic] (*Pseudoplesiops*). He later (Fowler, 1934) described two new monotypic pseudoplesiopine genera, *Loxopseudochromis* and *Opsipseudochromis*, from the Philippines.

Schultz (1943) described a new species, *Pseudoplesiops rosae*, from Rose Island, Phoenix Islands. He compared it with *P. typus* and assigned *Pseudoplesiops* to the Pseudochromidae, along with *Pseudochromis, Plesiops, Aporops* Schultz (now Serranidae) and *Pseudogramma*. He later (Schultz, 1953) synonymised *Nematochromis* with *Pseudoplesiops* and described an additional two species in the genus, *P. revellei* and *P. sargenti*. He also included acanthoclinids (now assigned to the Plesiopidae; see Mooi, 1993) in the Pseudochromidae.

Smith (1953) briefly described a new genus and species, *Chlidichthys johnvoelckeri* from east Africa. In the following year he reviewed pseudoplesiopsine [sic] fishes from south and east Africa (Smith, 1954). He ignored his

previous description and described *C. johnvoelckeri* again as a new genus and species, along with another new congener, *C. pembae*, and a second new genus and species, *Wamizichthys bibulus*. He also assigned *P. rosae* to *Chlidichthys*, and, in comparing *C. pembae* with similar species, noted that: "It will not be surprising if a careful examination of *Pseudoplesiops typus* Bleeker, and of *Nematochromis annae* Weber, prove them to be one and the same and identical with the above." He excluded Fowler's (1934) *Loxopseudochromis* and *Opsipseudochromis* to the Owstoniidae (now considered a synonym of the Cepolidae; see Gill & Mooi, 1993: 331).

Smith (1954) separated the Pseudoplesiopsinae from the Pseudochrominae, the only other pseudochromid subfamily he recognised, on the basis of the following characters: dorsal- and anal-fin spines weak and flexible (versus strong); most segmented rays in dorsal and anal fins simple (versus mostly or all branched); pelvic fins with a weak spine and three or four simple, segmented rays (versus with a spine and five branched, segmented rays); lateral line reduced to a tubed scale at the shoulder and at most a series of pitted scales along middle of side and peduncle (versus represented by an anterodorsal and a posterolateral series of tubed scales); dorsal and anal fins without basal scaly sheaths (versus with basal scaly sheaths); lower pectoral-fin proximal radial abutting against both coracoid and scapula (versus coracoid only); and vertebrae 11 + 16 (versus 10 + 16).

Böhlke (1960) recognised three separate families, Pseudochromidae, Anisochromidae and Pseudoplesiopidae, and included *Chlidichthys, Nematochromis, Pseudoplesiops* and *Wamizichthys* in the latter.

Norman (1966) included *P. typus* as sole member of the Pseudoplesiopinae, which he regarded as a subfamily of the Plesiopidae. He recognised the Pseudochrominae as a subfamily of the Serranidae, in which he placed *Nematochromis* [as well as *Pseudochromis, Dampieria, Nesiotes* De Vis (= *Cypho* Myers), *Pseudochromichthys* (= *Plesiops*, Plesiopidae; see Mooi, 1996), *Pseudocrenilabrus* Fowler (now in Cichlidae), *Pseudogramma* and *Gramma*].

Lubbock reviewed pseudochromids of the Red Sea and northwestern Indian Ocean (Lubbock, 1975), central Indian Ocean (Lubbock, 1976) and western Indian Ocean (Lubbock, 1977). He recognised a total of nine pseudoplesiopine species in these papers, six of which he described as new. He placed all of the species in *Chlidichthys*, including the monotypic *Wamizichthys*.

Springer *et al.* (1977) synonymised the Anisochromidae with the Pseudochromidae, and proposed that the Anisochromidae and Pseudoplesiopinae were more closely related to each other than either was to the Pseudochrominae. Springer *et al.* noted that several of Smith's (1954) pseudoplesiopine characters were shared with anisochromines, and were thus synapomorphies of the two subfamilies (fin spine development; reduction in number of pelvic-fin rays; presence of at least one unbranched pelvic-fin ray; absence of scale sheaths on dorsal and anal fins; and absence of tubed scales in posterolateral lateral line). They diagnosed the Pseudoplesiopinae by the following autapomorphies: all segmented pelvic-fin rays simple; segmented dorsal-fin rays mostly simple; single tubed lateral-line scale; ventralmost proximal radial of pectoral fin articulates with coracoid and scapula; and all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials.

Edwards & Randall (1983) placed *Chlidichthys* in junior synonymy with *Pseudoplesiops*, and described a distinctive new species from the Red Sea, *Pseudoplesiops lubbocki*.

Godkin & Winterbottom (1985) provided evidence for classification of the Congrogadidae, previously placed in the Blennioidei or Trachinoidei, as a subfamily of the Pseudochromidae, and the sister-group of the Anisochrominae; they proposed that the Pseudoplesiopinae is the sister-group of the Anisochrominae + Congrogadinae. In so doing, they noted that all of the synapomorphies proposed by Springer *et al.* (1977) to unite the Anisochrominae with the Pseudoplesiopinae were also found in the Congrogadinae. They also noted that one of the characters used by Springer *et al.* to diagnose the Pseudoplesiopinae was also found in the Congrogadinae (all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials), and that another was not found universally among pseudoplesiopines (ventralmost proximal radial of pectoral fin articulates with coracoid and scapula). They therefore concluded that only three of the pseudoplesiopine autapomorphies proposed by Springer *et al.* (1977) were valid: segmented pelvic-fin rays all simple; most segmented dorsal-fin rays simple; and a single tubed lateral-line scale. However, they overlooked that *Pseudoplesiops lubbocki* Edwards & Randall (1983) has mostly branched dorsal-fin rays.

Allen (1987) described three new species in the genus *Pseudoplesiops*: *P. multisquamatus, P. knighti, P. howensis*. He noted, however, that they exhibited characters that had been traditionally used to separate *Chlidichthys* from *Pseudoplesiops*. He therefore regarded the generic assignment of the three species provisional.

Gill *et al.* (1991) followed Schultz (1953) in placing *Nematochromis* in synonymy with *Pseudoplesiops*. They noted that the syntypes of *N. annae* represent two different, and otherwise undescribed, species. They therefore designated a lectotype for *N. annae*, and described the second species, *P. collare*, based on the paralectotype and an additional specimen (holotype) from Flores. They also noted that Schultz's *P. sargenti* is a junior synonym of *P. typus*.

Gill & Randall (1994) demonstrated monophyly for *Chlidichthys* (including all of the Red Sea and western and central Indian Ocean species recognised in Lubbock's papers) from synapomorphies associated with lower-lip and cephalic-laterosensory morphology, and described a new species from southern Oman, *C. cacatuoides*. They noted that *Pseudoplesiops lubbocki* was not referable to *Pseudoplesiops*, and that instead it shared some characters with *Chlidichthys*. They suggested that it should be placed in its own genus.

Materials and methods

Phylogenetic analyses were performed using the implicit enumeration option of Hennig86 version 1.5 (Farris, 1988). Character polarity was determined by outgroup comparison. The Anisochrominae + Congrogadinae were used as first outgroup following the scheme of relationships proposed by Godkin & Winterbottom (1985). *Assiculoides desmonotus* Gill & Hutchins and *Assiculus punctatus* Richardson were used as the second and third outgroups, respectively. Although both of these genera are currently classified in the Pseudochrominae, current evidence indicates that they form successive sister groups to a clade consisting of the Anisochrominae + Congrogadinae + Pseudoplesiopinae (Gill & Hutchins, 1997: 45).

Nomenclature of head pores follows Winterbottom (1986). When referring to fin rays, the term ray is used in its general sense to include both spinous (azygous, unsegmented, bilaterally fused) and soft rays.

Numerous pseudoplesiopine specimens and radiographs were examined for external (including superficial osteology) and post-cranial axial skeleton characters, respectively. These materials, which represented all known species, will be listed in our forthcoming generic revisions. Similarly, a more extensive listing of pseudochromine and non-pseudochromid specimens will be listed in a forthcoming paper on pseudochromid phylogeny and biogeography by the first author. The following cleared and stained pseudoplesiopine specimens (variously prepared following the methods of Taylor, 1967, Dingerkus & Uhler, 1977, and Potthoff, 1984) were examined (institutional codes follow Leviton *et al.*, 1985): *Amsichthys knighti*, AMS I.22612-034 (1: 28.3 mm SL), AMS I.21540-046 (3: 19.5–30.4 mm SL), ASIZ uncat. (2: 24.0–27.4 mm SL), USNM 306590 (1: 29.2 mm SL); *Chlidichthys* sp. 1, ROM uncat. (RW 88–15) (2: 33.5–38.1 mm SL); *C. auratus*, USNM 211780 (2: 37.5–37.8 mm SL); *C. bibulus*, BPBM 27310 (1: 26.8 mm SL); *C. cacatuoides*, BMNH 1994.4.19.1 (1 paratype: 37.2 mm SL); *C. inornatus*, AMS I.23653-002 (1: 27.9 mm SL), ROM CS857 (3: 30.0–37.0 mm SL); *C. johnvoelckeri*, CAS 35451 (2: 24.7–37.9 mm SL), ROM uncat. (RW 88–26) (2: 36.2–38.7 mm SL); *C. pembae*, ROM uncat. (RW 88–15) (2: 21.2–23.3 mm SL); *C. rubiceps*, USNM 211777 (5: 12.0–15.0 mm SL), BMNH 1999.1.14.18 (1: 27.2 mm SL); *Lubbockichthys* sp. 1, AMS I.25107-067 (1: 47.3 mm SL); *L.* sp. 2, AMS I.39406-001 (1: 44.6 mm SL); *L.* sp. 3, AMS I.39407-001 (1: 37.2 mm SL); *L. multisquamatus*, AMS I.20779-175 (1: 36.3 mm SL); *Pectinochromis lubbocki*, BPBM 28119 (1 paratype: 35.5 mm SL); *Pseudoplesiops* sp. 1, AMS I.20756-014 (1: 25.7 mm SL); *P.* sp. 2, BMNH 1999.1.14.17 (1: 22.6 mm SL); *P. annae*, AMS I.21918-017 (1: 21.0 mm SL), USNM 270268 (2: 24.2–29.3 mm SL); *P. howensis*, AMS I.19755-024 (1: 21.0 mm SL); *P. rosae*, AMS I.22582-034 (3: 17.2–22.0 mm SL), BMNH 1999.1.14.14-16 (3: 18.0–21.4 mm SL); *P. typus*, AMS I.19442-013 (1: 50.6 mm SL), ROM CS585 (1: 49.0 mm SL). Our discussions of the morphology of immediate outgroups are largely based on details provided by Springer *et al.* (1977), Godkin & Winterbottom (1985) and Winterbottom (1986, 1996), and on the following cleared and stained specimens: ANISOCHROMINAE: *Anisochromis kenyae*, RUSI 4906 (1: 23.3 mm SL); *A. straussi*, USNM 215859 (4 paratypes: 19.0–24.0 mm SL), USNM 257761 (1: 8.0 mm SL). CONGROGADINAE: *Blennodesmus scapularis*, AMS I.26723-087 (2: 49.7–54.1 mm SL), BMNH uncat. (1: 29.6 mm SL); *Congrogadus spinifer*, BMNH 1911.1.4.3-4 (1: c. 122 mm SL); *Congrogadus subducens*, AMS I.26723-051 (1: 49.3 mm SL), AMS I.26723-052 (1: 18.7 mm SL), AMS I.26723-057 (1: 135.0 mm SL), BMNH 1847.7.21.67-69 (1: c. 147 mm SL); *Halidesmus scapularis*, BMNH 1933.10.31.1-4 (1: c. 114 mm SL); *Haliophis guttatus*, BMNH 1951.1.16.606-608 (1: c. 82 mm SL). PSEUDOCHROMINAE: *Assiculoides desmonotus*, WAM P.30929-008 (2 paratypes: 41.3–46.2 mm SL); *Assiculus punctatus*, AMS I.13113 (1: 63.0 mm SL), NTM S.10016-009 (4: 21.7–51.9 mm SL).

Subfamily Pseudoplesiopinae

Pseudoplesiopini Bleeker, 1875: 4.

Diagnosis. Members of the subfamily are diagnosed by the following synapomorphies: single tubed lateral-line scale (character 1); posterior part of pelvic bone with triangular or hook-shaped lateral process for attachment of slip of hypaxial musculature (character 2); base of anterior process on pelvic bone posteriorly positioned (character 3); coracoid articulates ventrally with medial face of lateral lamina of cleithrum (character 4); basihyal bound to anterior face of basibranchial 1 (character 5); urohyal with prominent dorsally directed process (character 6). Two additional characters provide equivocal support for monophyly of the subfamily: dorsal profile of anterior ceratohyal straight, without excavation (remnant of beryciform foramen, sensu McAllister, 1968); and all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials. Both characters also occur in the Congrogadinae, but not in the Anisochrominae, their sister group. Therefore, they may be independent autapomorphies of the Congrogadinae and Pseudoplesiopinae, or they may be synapomorphies of the more inclusive Anisochrominae + Congrogadinae + Pseudoplesiopinae clade that have undergone "reversal" in the Anisochrominae. These two characters will be discussed in greater detail in a forthcoming paper on pseudochromid intrarelationships and biogeography by the first author.

Diagnoses of pseudoplesiopine genera

Lubbockichthys n.gen.

Figs. 1, 9A, 10A, 12A, 13A, 14A

Type species. *Pseudoplesiops multisquamatus* Allen, 1987.

Diagnosis. *Lubbockichthys* is distinguished from other pseudoplesiopines by the following four autapomorphies: parietal enclosing dorsal part of supratemporal laterosensory canal (character 7; also occurs homoplastically in *Pseudoplesiops howensis*); scales cycloid at all stages of ontogeny (character 8); scales small, scales in lateral series 51–66 (character 9); and some head bones with weakly honeycombed surface (character 10). Two other characters provide equivocal support for monophyly of the genus (see

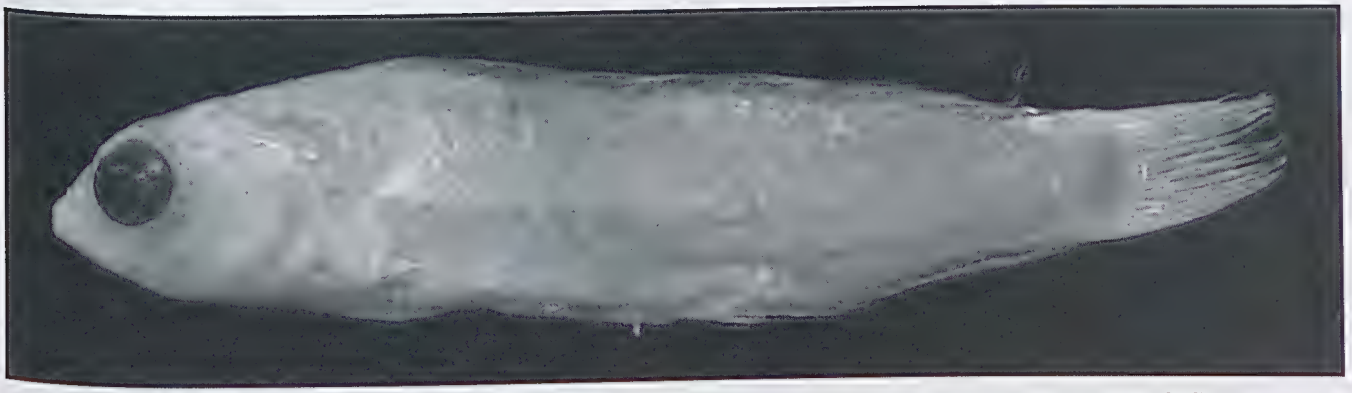

Figure 1. *Lubbockichthys multisquamatus*, WAM P.27470-002, 41.7 mm SL, holotype, Escape Reef, Great Barrier Reef.

Results of Parsimony Analysis below). The first of these, posterior interorbital pore present (character 23, state 0), is either an autapomorphy of *Lubbockichthys*, or diagnoses (state 1) a clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops*. The second character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious optimisations on the proposed phylogeny, one of which optimises mostly branched rays as an autapomorphy of *Lubbockichthys* (and homoplastically of *Pectinochromis*). Other characters useful in identifying *Lubbockichthys* are summarised in Table 2.

Included nominal species. *Pseudoplesiops multisquamatus* Allen, 1987.

Geographic distribution. Eastern Indian Ocean to the central Pacific, from the Cocos-Keeling Islands, east to the Line Islands, south to New Caledonia and north to the Ryukyu Islands.

Justification for erection of new genus. Erection of *Lubbockichthys* is justified because it establishes a monophyletic classification; species assigned to *Lubbockichthys* cannot be assigned to any other pseudoplesiopine genus without rendering that genus para- or polyphyletic. The erection of *Lubbockichthys* also draws attention to the morphological distinctiveness of the genus (and thus acknowledges a morphological gap).

Etymology. Named for the late Dr Hugh Roger Lubbock, in combination with the Greek *ichthys*, meaning fish, in recognition of Dr Lubbock's contributions to the systematics of pseudochromid fishes. Gender is masculine.

Pseudoplesiops Bleeker

Figs. 2, 9B, 10B, 11B, 12B, 13B, 14B

Pseudoplesiops Bleeker, 1858: 215 (type species, *Pseudoplesiops typus* Bleeker, by monotypy).
Nematochromis Weber, 1913: 264 (type species, *Nematochromis annae* Weber, by monotypy).

Diagnosis. *Pseudoplesiops* is demonstrably monophyletic in having the medial laminae of the pelvic bones expanded dorsally (character 11). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Nematochromis annae* Weber, 1913; *Pseudoplesiops collare* Gill, Randall & Edwards, 1991; *P. howensis* Allen, 1987; *P. revellei* Schultz, 1953; *P.*

Figure 2. *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL, Ashmore Reef, Timor Sea.

rosae Schultz, 1943; *P. sargenti* Schultz, 1953; *P. typus* Bleeker, 1858.

Geographic distribution. Central Indian Ocean to the central Pacific, from the Maldive Islands, east to Oeno Atoll, north to the Ryukyu Islands and south to Lord Howe Island.

Etymology. From the Greek *pseudos*, false, and *Plesiops*, a genus of plesiopid fish, alluding to the purported similarity between the type species, *P. typus*, and *Plesiops*. Gender is masculine.

Amsichthys n.gen.

Figs. 3, 9C, 10C, 11A, 12C, 13C, 14C

Type species. *Pseudoplesiops knighti* Allen, 1987.

Diagnosis. *Amsichthys* is demonstrably monophyletic in lacking the upper preopercular pore (character 12). Monophyly of the genus is also supported by a single homoplastic character that also occurs in *Pectinochromis*: eyes large (character 30; see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops knighti* Allen, 1987.

Geographic distribution. Eastern Indian Ocean and West Pacific, from the west coast of Thailand, east to the Solomon Islands, south to the Great Barrier Reef and north to the Ryukyu Islands.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Amsichthys* as the sister group of *Pseudoplesiops*. Thus, it could be included within *Pseudoplesiops* without affecting the monophyletic status of that genus. However, we believe that character evidence for a sister relationship between the two genera is weak; such a relationship is supported by a single character, third supraneural bone well developed (character 25, state 1), but this varies among *Pseudoplesiops* species and intraspecifically in a *Chlidichthys* species (see *Results of Parsimony Analysis*). It is possible that additional characters might lead to a different phylogenetic position for *Amsichthys*; indeed, a different interpretation of characters 12 and 28, such that the reduction in number of preopercular pores was seen as homologous, would lead to *Chlidichthys* + *Pectinochromis* forming the sister of *Amsichthys*. We therefore believe that the erection of *Amsichthys* will ultimately lead to greater nomenclatural stability, as its placement as the sister to any other pseudoplesiopine genus or clade of genera will not affect the generic assignment of its constituent species.

Erection of *Amsichthys* is also partly justified on the basis of its morphological distinctiveness.

Etymology. The generic name is a combination of AMS, the standard institutional code in ichthyology for the Australian Museum, Sydney, and the Greek *ichthys*, fish. It acknowledges the generous help, encouragement and friendship given by staff of the Australian Museum's Ichthyology Section to the first author during this study and throughout his career and training. Gender is masculine.

Chlidichthys Smith

Figs. 4, 6B, 7B, 8B, 9D, 10D, 12D, 13D, 14D

Chlidichthys Smith, 1953: 518 (type species: *Chlidichthys johnvoelckeri* Smith, 1953, by monotypy).
Wamizichthys Smith, 1954: 205 (type species: *Wamizichthys bibulus* Smith, 1954, by original designation and monotypy).

Diagnosis. *Chlidichthys* is distinguished from other pseudoplesiopines and demonstrably monophyletic in having two autapomorphies: lower lip interrupted at symphysis (character 13); and second infraorbital bone absent (character 26, state 2). Two other characters, 31 (state 0; mostly unbranched dorsal-fin rays) and 32 (state 1; mostly unbranched anal-fin rays), provide equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Chlidichthys abruptus* Lubbock, 1977; *C. auratus* Lubbock, 1975; *Wamizichthys bibulus* Smith, 1954; *C. cacatuoides* Gill & Randall, 1994; *C. inornatus* Lubbock, 1976; *C. johnvoelckeri* Smith, 1953;

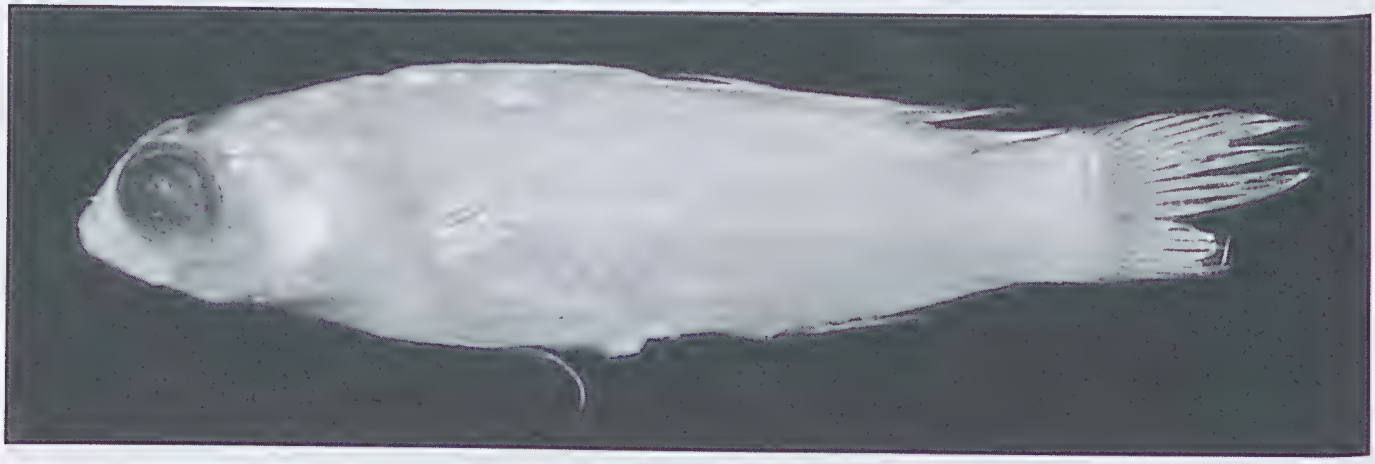

Figure 3. *Amsichthys knighti*, NTM S.11384-018, North Reef, Timor Sea.

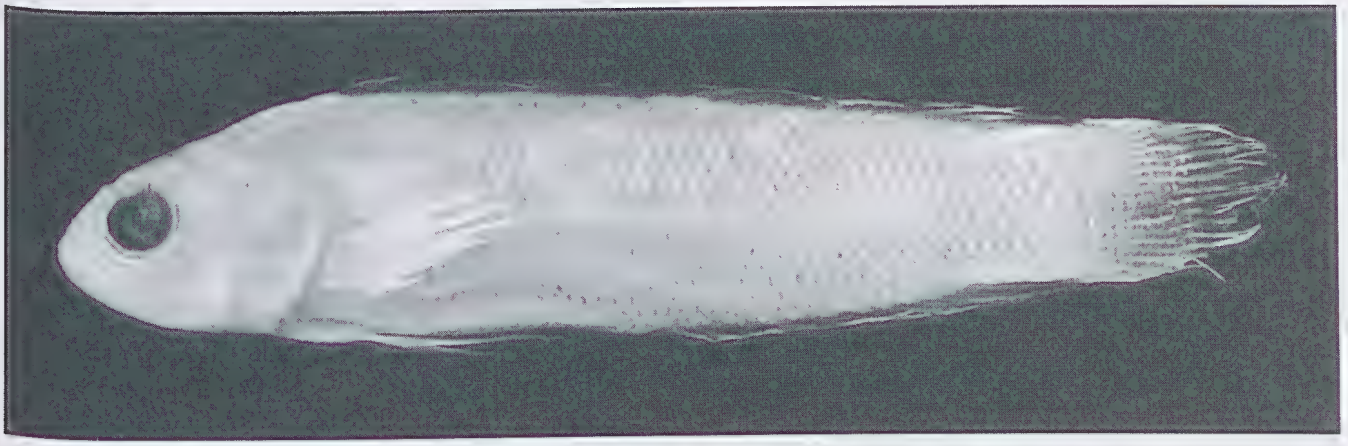

Figure 4. *Chlidichthys johnvoelckeri*, CAS 35451, 45.7 mm SL, Grande Comore Island, Comoro Islands.

C. pembae Smith, 1954; *C. randalli* Lubbock, 1977; *C. rubiceps* Lubbock, 1975; *C. smithae* Lubbock, 1977.

Geographic distribution. Western Indian Ocean, from the northern Red Sea and east Africa, north to southern Oman, east to Sri Lanka and south to Natal, South Africa.

Etymology. Apparently from the Greek *chlidanos*, delicate or luxurious, and *ichthys*, fish. Gender is masculine.

Pectinochromis n.gen.

Figs. 5, 9E, 10E, 12E, 13E, 14E

Type species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Diagnosis. *Pectinochromis* is distinguished from other pseudoplesiopine genera and demonstrably monophyletic in having six autapomorphies: first dorsal-fin pterygiophore expanded anteriorly (character 14); first dorsal-fin pterygiophore with lateral processes (character 15); second pterygiophore of dorsal fin inserts between neural spines 3 and 4 (character 16); dorsal fin anteriorly positioned (character 17); single supraneural bone (character 18); gill rakers relatively numerous (character 19). Monophyly of the genus is also supported by a single homoplastic character, eyes large (character 30), that also occurs in *Amsichthys*. Another homoplastic character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious character optimisations within the Pseudoplesiopinae; two of the optimisations identify it as an autapomorphy of *Pectinochromis*. The presence of mostly branched anal-fin rays (character 32) also provides equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below for discussion of this and the previous two characters). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Geographic distribution. Red Sea.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Pectinochromis* as the sister group of *Chlidichthys*; this relationship is strongly supported by five synapomorphies (see *Results of Parsimony Analysis* below). Thus, *Pectinochromis* could be included within *Chlidichthys* without affecting the monophyletic status of that genus. However, our decision to erect *Pectinochromis* is to draw attention to the morphological distinctiveness of the two genera. *Pectinochromis* is particularly distinctive, and is readily distinguished from all other pseudochromids by its unusual dorsal-fin and gill-raker morphology.

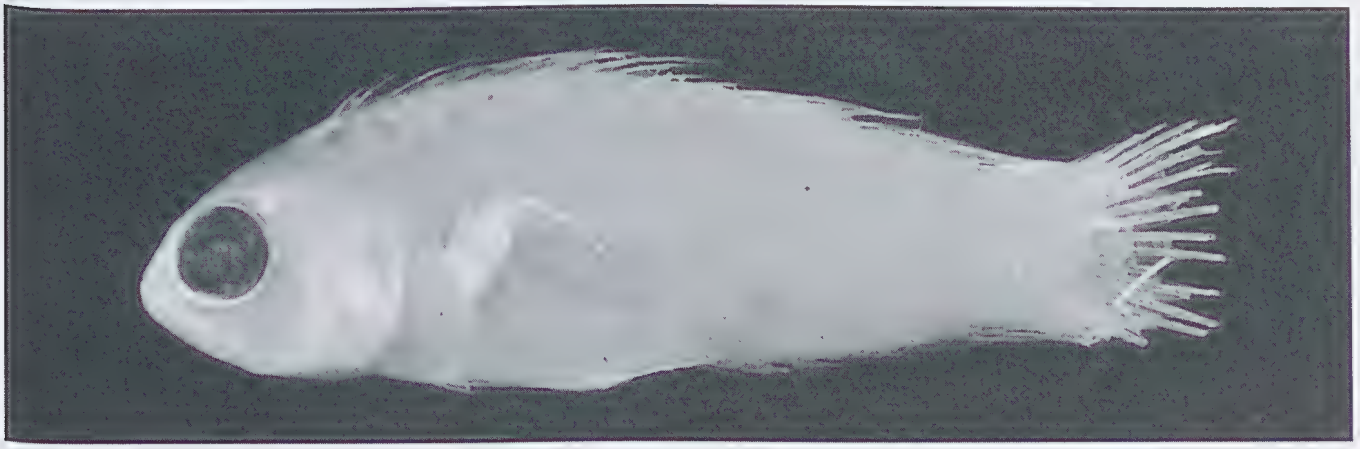

Figure 5. *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL, Gulf of Aqaba, Red Sea.

Table 1. Matrix of 32 characters of pseudoplesiopine genera (see text for details of characters).

	character number																			
						1							2					3		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
outgroup	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0
Lubbockichthys	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Pseudoplesiops	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
Amsichthys	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Chlidichthys	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
Pectinochromis	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0

Etymology. The generic name is from the Latin *pecten*, a comb or rake, and the Greek *Chromis*, a genus of pomacentrid fish, which has been used as a suffix for various pseudochromid genera (e.g., *Pseudochromis* and *Nematochromis*), and alludes to the relatively high number of gill rakers. Gender is feminine, in keeping with the accepted gender of *Chromis* [see Opinion 1417 (International Commission on Zoological Nomenclature, 1986) for ruling on the gender of *Chromis*].

Phylogenetic relationships

Character descriptions. A summary of character state distributions is given in Table 1.

Character 1. Single tubed anterior lateral-line scale. Pseudochromines and anisochromines have a series of tubed scales in the anterior portion of the lateral line (state 0). Pseudoplesiopines usually have only a single tubed scale, which is situated near the branchial opening (state 1; occasional specimens of *Lubbockichthys* species may have two tubed scales on one or both sides of the body). Congrogadines vary somewhat in the structure of their lateral line, but most have a single, anterodorsal lateral line consisting of a series of tubed scales (exceptions are *Rusichthys*, which lacks a lateral line, *Halidesmus*, which has three lateral lines, and *Halimuraenoides*, some *Halimuraena* species, one *Haliophis* species and occasional specimens of some *Congrogadus* species, all of which have two lateral lines, one anterodorsal, the other midlateral). The state found in pseudoplesiopines is regarded as apomorphic.

Character 2. Posterior part of pelvic bone with triangular or hook-shaped lateral process. Pseudochromines, anisochromines and congrogadines lack lateral processes on the posterior part of the pelvic bone (state 0; Fig. 6A). Pseudoplesiopines have a triangular or hook-shaped lateral process on the posterior part of the pelvic bone, which serves as an attachment site for a slip of hypaxial musculature (state 1; Fig. 6B). This arrangement is regarded as apomorphic.

Character 3. Base of anterior process on pelvic bone posteriorly positioned. The base of the anterior process (sensu Stiassny & Moore, 1992) of the pelvic bone of pseudochromines and anisochromines is positioned slightly to well anterior to the anterior edge of the pelvic-fin spine base (Fig. 6A; state 0). Congrogadines examined by us lack an anterior process on the pelvic bone. In pseudoplesiopines, the anterior process is positioned noticeably posterior to the anterior edge of pelvic-fin spine base (Fig. 6B; state 1). The latter state is regarded as apomorphic.

Character 4. Coracoid articulates ventrally with medial face of lateral lamina of cleithrum. In pseudochromines, anisochromines and congrogadines the ventral process of the coracoid attaches to the lateral face of a medial lamina on the cleithrum (Fig. 7A; state 0), whereas in pseudoplesiopines the coracoid attaches to the medial face of a lateral lamina (Fig. 7B; state 1). The latter state is regarded as apomorphic.

Character 5. Basihyal bound to anterior face of basibranchial 1. The basihyal loosely overlies basibranchial 1 in pseudochromines and anisochromines (Fig. 8A,C; state 0). It is tightly bound by connective tissue to the anterior face of basibranchial 1 in pseudoplesiopines (Fig. 8B; state 1). The basihyal is bound more-or-less tightly to basibranchial 1 in congrogadines (Fig. 8D), but the arrangement does not appear to be homologous with the condition found in pseudoplesiopines. Most notably, the condition in congrogadines differs in that there are two articulation points between the two bones, a dorsal attachment between the mid-dorsal face of basibranchial 1 and the posterior tip of the basihyal, and a ventral attachment between the anterior (cartilaginous) tip of basibranchial 1 and the posteroventral edge of the basihyal. In the latter attachment, the basihyal is embraced by small lateral projections that extend anteriorly from basibranchial 1 (and obscure the anterior cartilage tip from lateral view). The congrogadine condition is associated with a very different arrangement of the basibranchial 1/urohyal articulation, where the urohyal is positioned farther posteriorly (as it is also in anisochromines), articulating with a posteroventral process from basibranchial 1 (versus weakly associated with the anterior cartilage tip of basibranchial 1 in pseudochromines and pseudoplesiopines). We consider the basihyal/basibranchial 1 arrangement displayed by pseudoplesiopines to be apomorphic within the Pseudochromidae.

Character 6. Urohyal with prominent dorsally directed process. The urohyal of pseudochromines has a small to moderately developed posterodorsally directed process, which is weakly embraced by anteroventrally projecting processes from the hypobranchials 1 (Fig. 8A; state 0).

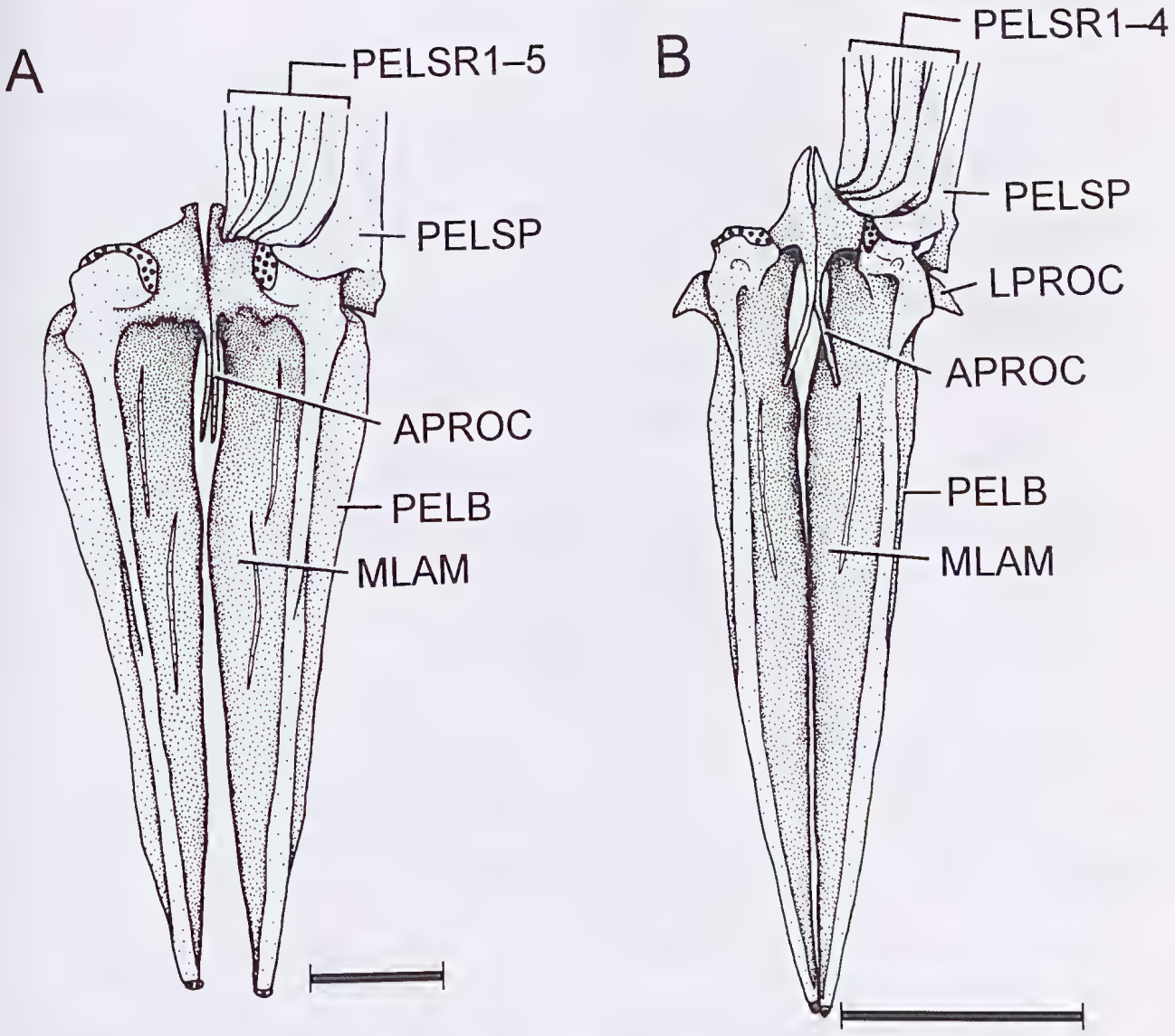

Figure 6. Pelvic girdles of two pseudochromid species in ventral view: A, "*Pseudochromis*" cf. *paccagnellae* (Pseudochrominae), AMS I.22613-008, 46.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Anterior to bottom of page; cartilage shown in large stipple. Abbreviations: APROC, anterior process; LPROC, lateral process; MLAM, medial lamina; PELB, pelvic bone; PELSP, pelvic-fin spine; PELSR1–5, pelvic segmented rays 1–5. Scale bars = 1 mm.

Pseudoplesiopines have a prominent dorsal process on the urohyal, which is also embraced by anteroventral processes from the hypobranchials 1, but it is dorsally rather than posterodorsally directed (Fig. 8B; state 1). Anisochromines and congrogadines lack a dorsal process from the urohyal to the hypobranchials 1; the urohyal is well separated from the hypobranchials, and the hypobranchials have small posteroventrally (rather than anteroventrally) projecting processes (Fig. 8C,D). The condition shown by pseudoplesiopines is considered apomorphic within the Pseudochromidae.

Character 7. Parietal bears enclosed lateral-line canal. In *Chlidichthys, Amsichthys, Pectinochromis* and most *Pseudoplesiops*, the dorsal portion of the supratemporal lateral-line commissure passes over the parietal as a membranous canal, which is either unossified or ossified medially only (Fig. 9B–E; state 0). In *Lubbockichthys* and *Pseudoplesiops howensis*, the dorsal portion of the supratemporal lateral-line commissure passes through a fully ossified (enclosed) canal in the parietal (Fig. 9A; state 1). In *Assiculoides* and *Assiculus*, the supratemporal commissure passes over the parietal in a membranous tube that is either unossified or medially ossified only; anisochromines have similar ossification of the canal, but the commissure is heavily branched and continuous across the dorsal midline. In congrogadines, the commissure is also continuous across the dorsal midline, but is mostly ossified throughout its length. As far as we can ascertain, the ossified portion is separate from, though closely applied to, the parietal bone. We therefore consider the condition shown by *Lubbockichthys* and *P. howensis* apomorphic.

Character 8. Scales "cycloid" at all stages of ontogeny. *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* have cteni on posterior body scales, at

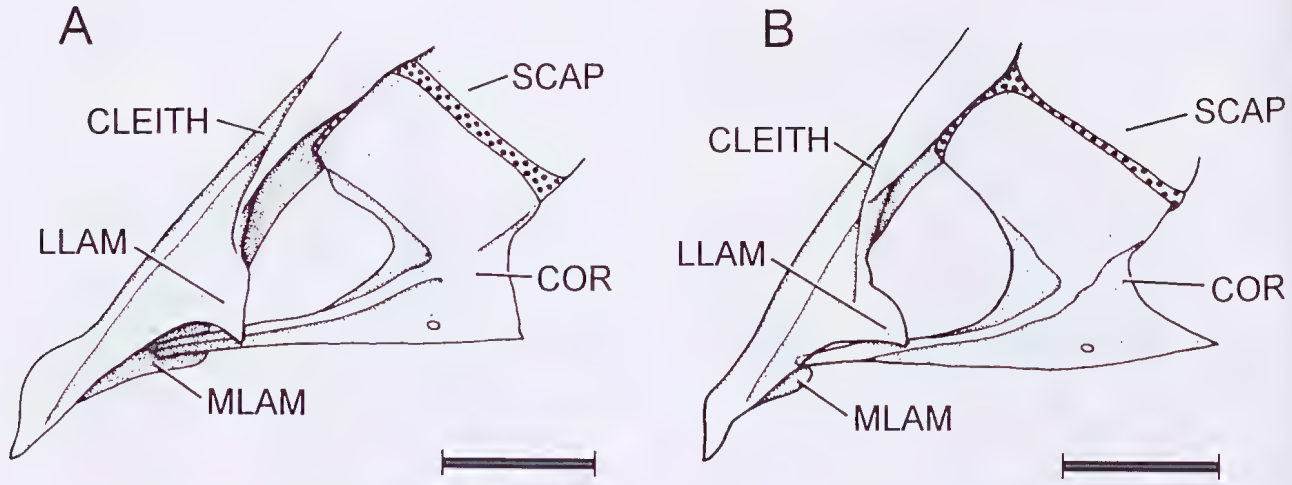

Figure 7. Right lateral view (reversed) of lower part of pectoral girdle of two pseudochromid species: A, "*Pseudochromis*" *diadema* (Pseudochrominae), USNM 210017, 35.0 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Abbreviations: CLEITH, cleithrum; COR, coracoid; MLAM, medial lamina of cleithrum; LLAM, lateral lamina of cleithrum; SCAP, scapula. Scale bars = 1 mm.

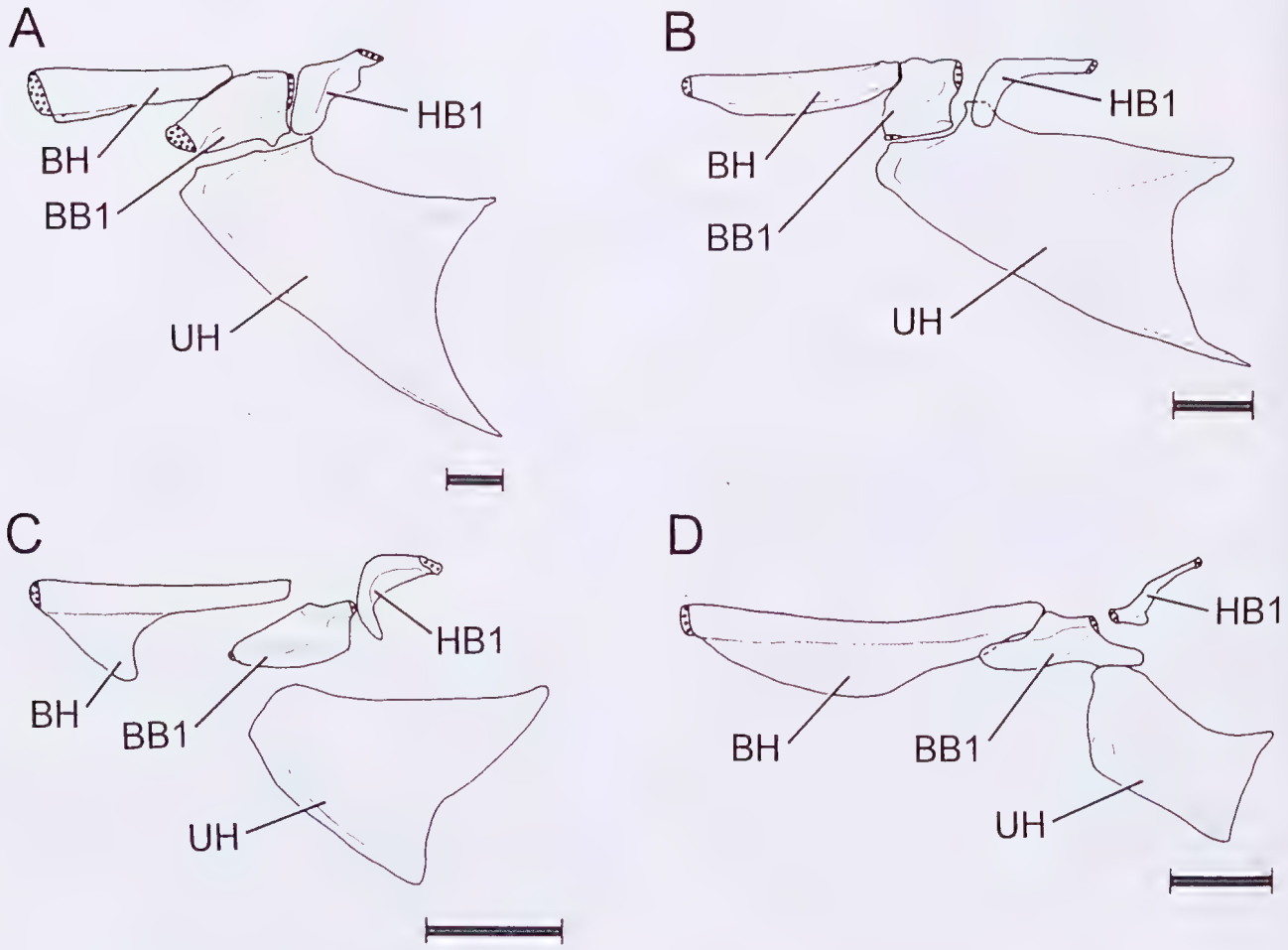

Figure 8. Right lateral view (reversed) of basihyal (BH), basibranchial 1 (BB1), hypobranchial 1 (HB1) and urohyal (UH) of selected pseudochromid species: A, *Assiculus punctatus* (Pseudochrominae), NTM S.10016-009, 32.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL; C, *Anisochromis kenyae* (Anisochrominae), RUSI 4906, 23.3 mm SL; D, *Blennodesmus scapularis* (Congrogadinae), AMS I.26723-087, 49.7 mm SL. Cartilage shown in large stipple. Scale bars = 0.5 mm.

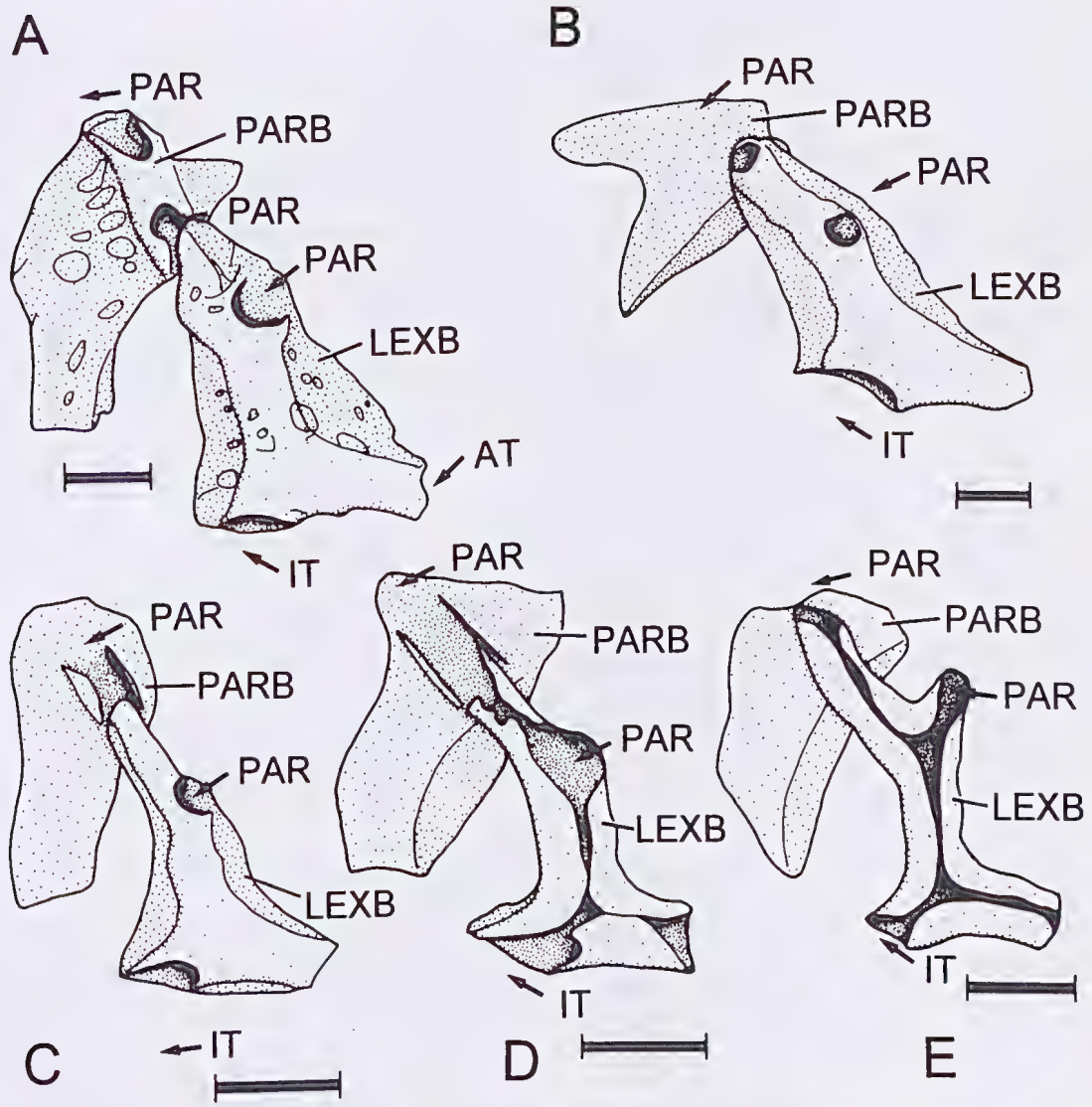

Figure 9. Lateral extrascapulae and parietal bones and associated laterosensory pores of selected pseudoplesiopine species: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate locations of sensory pores. Abbreviations: AT, anterior temporal pore; IT, intertemporal pore; LEXB, lateral extrascapular bone; PAR, parietal pore; PARB, parietal bone. Scale bars = 0.5 mm.

least as juveniles (state 0), as do pseudochromines and anisochromines and the vast majority of perciforms. Species of *Lubbockichthys* are unique among pseudoplesiopines in lacking cteni on body scales at all stages of ontogeny (state 1). The posterior body scales of congrogadines also lack cteni, as do those of some perciform taxa, such as ambassids, bathyclupeids, carangoids, cepolids, dinolestids, lactariids, leiognathids, opistognathids, sinipercids, clinids, dactyloscopids, zoarcoids, and most cirrhitoids (see Johnson, 1984: table 120; Roberts, 1993: appendix 1). Such scales have been generally termed "cycloid", but they are not homologous with the cycloid scales of lower teleosts (J. Radding, pers. comm.). Cteni are present in small (less than about 30 mm SL) specimens of *Pseudoplesiops typus*, but are absent from larger specimens; presumably cteni are either shed or, more likely, resorbed with growth. Other species of *Pseudoplesiops* retain cteni on posterior body scales throughout ontogeny. We regard the condition found in *Lubbockichthys* as apomorphic and nonhomologous with that found in *P. typus*.

Character 9. Scales small. *Chlidichthys*, *Amsichthys*, *Pectinochromis* and *Pseudoplesiops* have relatively large to moderately small scales (state 0). In contrast, *Lubbockichthys* has relatively small scales (state 1). This character can be seen by differences in numbers of scales in lateral series (Table 2): 37–52 in *Chlidichthys*, 30–33 in *Amsichthys*, 35–39 in *Pectinochromis* and 26–42 in *Pseudoplesiops*, versus 51–66 in *Lubbockichthys*. Most of the outgroup taxa have relatively large to moderately small scales. Scales in lateral series counts range from 39–44 in anisochromines, 35–42 in *Assiculoides*, and 38–46 in *Assiculus*. However, congrogadines also have numerous, small scales. Nevertheless,

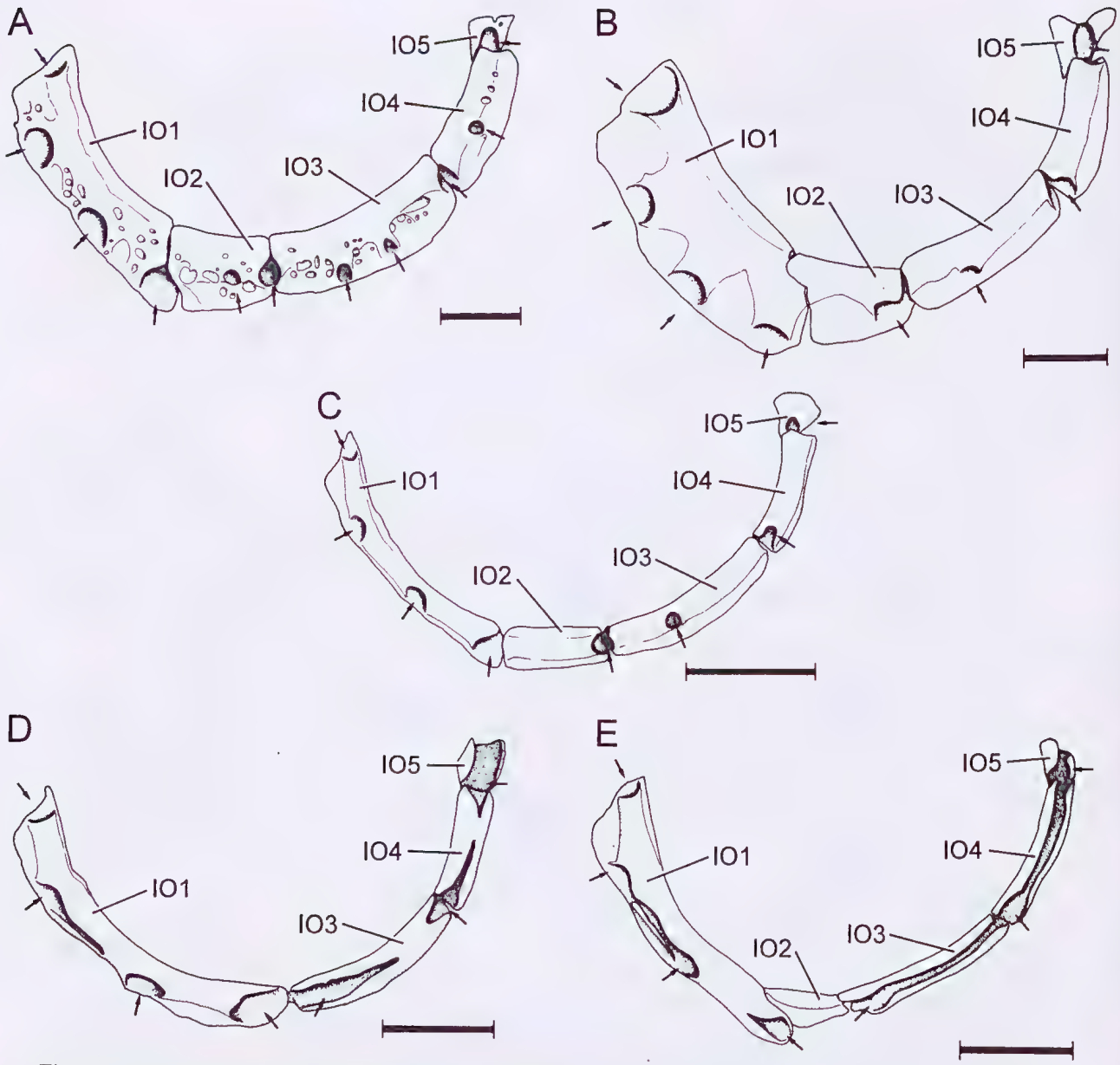

Figure 10. Infraorbital bones (IO1-5) of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, ROM CS585, 49.0 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate positions of suborbital pores. Scale bars = 1 mm.

the condition shown by *Lubbockichthys* is most parsimoniously argued to be derived within the Pseudoplesiopinae.

Character 10. Some head bones with weakly honeycombed surface. Pseudoplesiops, Amsichthys, Pectinochromis and *Chlidichthys* have relatively smooth head bones (e.g., Figs. 9B–E, 10B–E; state 0), as do the outgroup taxa. *Lubbockichthys* has at least some head bones with a weakly honeycombed surface (e.g., Figs. 9A, 10A; state 1). We consider this condition to be apomorphic within the Pseudoplesiopinae.

Character 11. Medial laminae of pelvic bones expanded dorsally. The medial laminae (= inner wing of Stiassny & Moore, 1992) of the pelvic bones of *Lubbockichthys, Amsichthys, Chlidichthys* and *Pectinochromis* are at most weakly expanded dorsally, so that the pelvic bones have a concave to weakly convex dorsal profile (Fig. 11A; state 0). The medial laminae of the pelvic bones of *Pseudoplesiops* are strongly expanded dorsally, so that the bones have a strongly convex dorsal profile (Fig. 11B; state 1). Anisochromines and the basal congrogadine genus *Rusichthys* have dorsally expanded medial laminae (with the exception of *Halidesmus scapularis*, more derived congrogadine genera lack dorsally expanded medial laminae, but this appears to be associated with reduction or loss of the pelvic fin), whereas *Assiculoides* and *Assiculus* (and all other pseudochromines) have weakly expanded laminae on the pelvic bones. Because both states occur in the outgroup taxa, this character was not polarised.

Character 12. Loss of uppermost preopercular pore. Lubbockichthys, Pseudoplesiops, Pectinochromis and *Chlidichthys* and the outgroup taxa have the uppermost preopercular pore associated with the terminal opening in the preopercle (Fig. 12A,B,D,E; state 0). *Amsichthys* is distinctive in usually lacking a pore at the dorsal terminus of the preopercle (Fig. 12C; state 1). We consider the absence of the dorsal pore apomorphic. A terminal pore was present on one or both sides of the head of a few, relatively large specimens of *Amsichthys*; in contrast, a terminal pore was consistently present in juveniles and adults of the other pseudoplesiopine genera and in the outgroups. This suggests that the pore may develop relatively late in ontogeny in *Amsichthys*, in which case the character should be redescribed as delayed development of uppermost preopercular pore rather than loss of uppermost preopercular pore.

Character 13. Lower lip interrupted at symphysis. Amsichthys, Lubbockichthys, Pectinochromis, Pseudoplesiops, anisochromines, congrogadines, *Assiculoides* and *Assiculus* have the lower lip uninterrupted at the symphysis (Gill & Randall, 1994: fig. 1A; Gill & Hutchins, 1997: fig. 4; state 0). *Chlidichthys* species are unique among pseudoplesiopines in having the lower lip interrupted at the symphysis (Gill & Randall, 1994: fig. 1B; state 1). We consider the latter condition apomorphic.

Character 14. First dorsal-fin pterygiophore expanded anteriorly. The anterior face of the first dorsal-fin pterygiophore is at best weakly expanded anteriorly in *Chlidichthys, Amsichthys, Lubbockichthys* and *Pseudoplesiops* (Fig. 13A–D; state 0). *Pectinochromis* is unusual in having the anterior part of the first dorsal-fin pterygiophore strongly expanded anteriorly (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* have the anterior face of the first pterygiophore weakly expanded anteriorly; congrogadines lack the homologue of the first dorsal-fin pterygiophore (Gill, 1998). We therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 15. First dorsal-fin pterygiophore with lateral processes. Chlidichthys, Amsichthys, Lubbockichthys and *Pseudoplesiops* lack lateral processes on the first dorsal-fin pterygiophore (Fig. 13A–D; state 0). *Pectinochromis* is distinctive in having prominent lateral processes on the first dorsal-fin pterygiophore (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* lack such processes (and, as noted above, congrogadines lack the homologue of the first pterygiophore), and we therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 16. Second dorsal-fin pterygiophore insertion between neural spines 2 and 3. Chlidichthys, Amsichthys, Lubbockichthys, Pseudoplesiops, anisochromines, *Assiculus* and *Assiculoides* have the first dorsal-fin pterygiophore insertion between neural spines 2 and 3, and the next two pterygiophores between neural spines 3 and 4 (Fig. 13A–D; state 0). Congrogadines have only two dorsal-fin pterygiophores inserting anterior to neural spine 4, both positioned between neural spines 3 and 4, owing to the loss of the first pterygiophore (Gill, 1998). *Pectinochromis* has the first two pterygiophores between neural spines 2 and 3, and the third pterygiophore between neural spines 3 and 4 (Fig. 13E; state 1). The anterior position of the second pterygiophore is regarded as apomorphic.

Character 17. Dorsal fin anteriorly positioned. The dorsal-fin origin of *Lubbockichthys, Pseudoplesiops, Amsichthys* and *Chlidichthys* is near the vertical through the posterior edge of the operculum (Figs. 1–4, 12A–D; state 0), as it is in the outgroup taxa. *Pectinochromis* is unusual in having the dorsal-

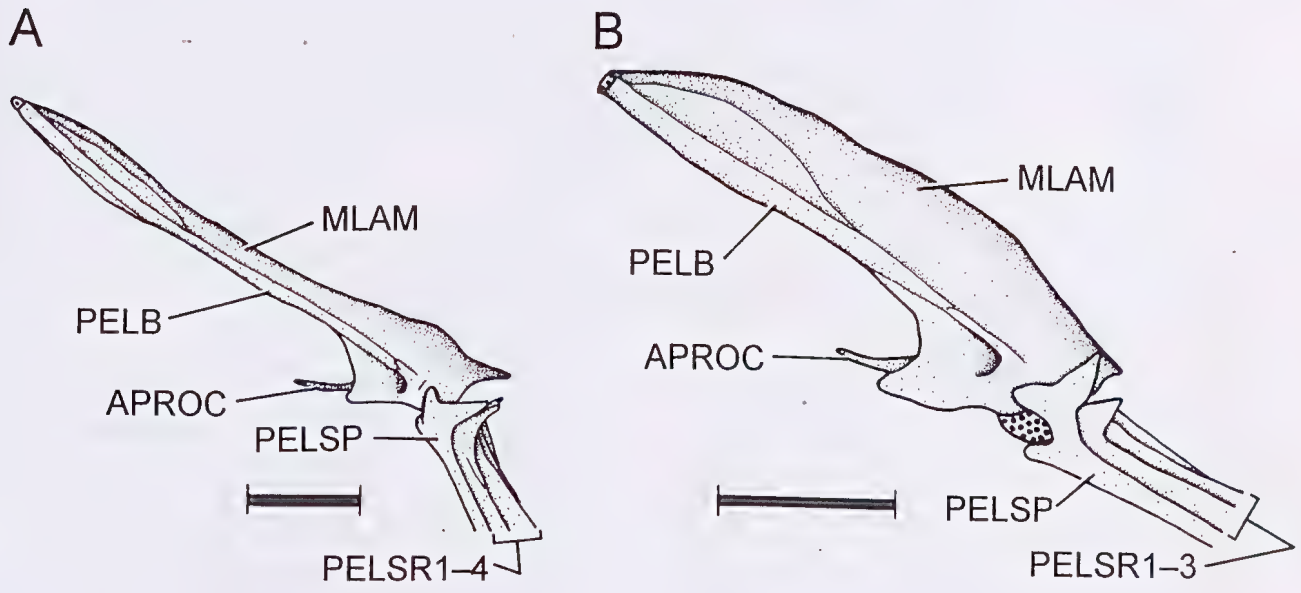

Figure 11. Right lateral view (reversed) of pelvic girdles of two pseudoplesiopine species: A, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; B, *Pseudoplesiops rosae*, AMS I.22582-073, 22.0 mm SL. Abbreviations as in Fig. 1. Cartilage shown in large stipple. Scale bars = 0.5 mm.

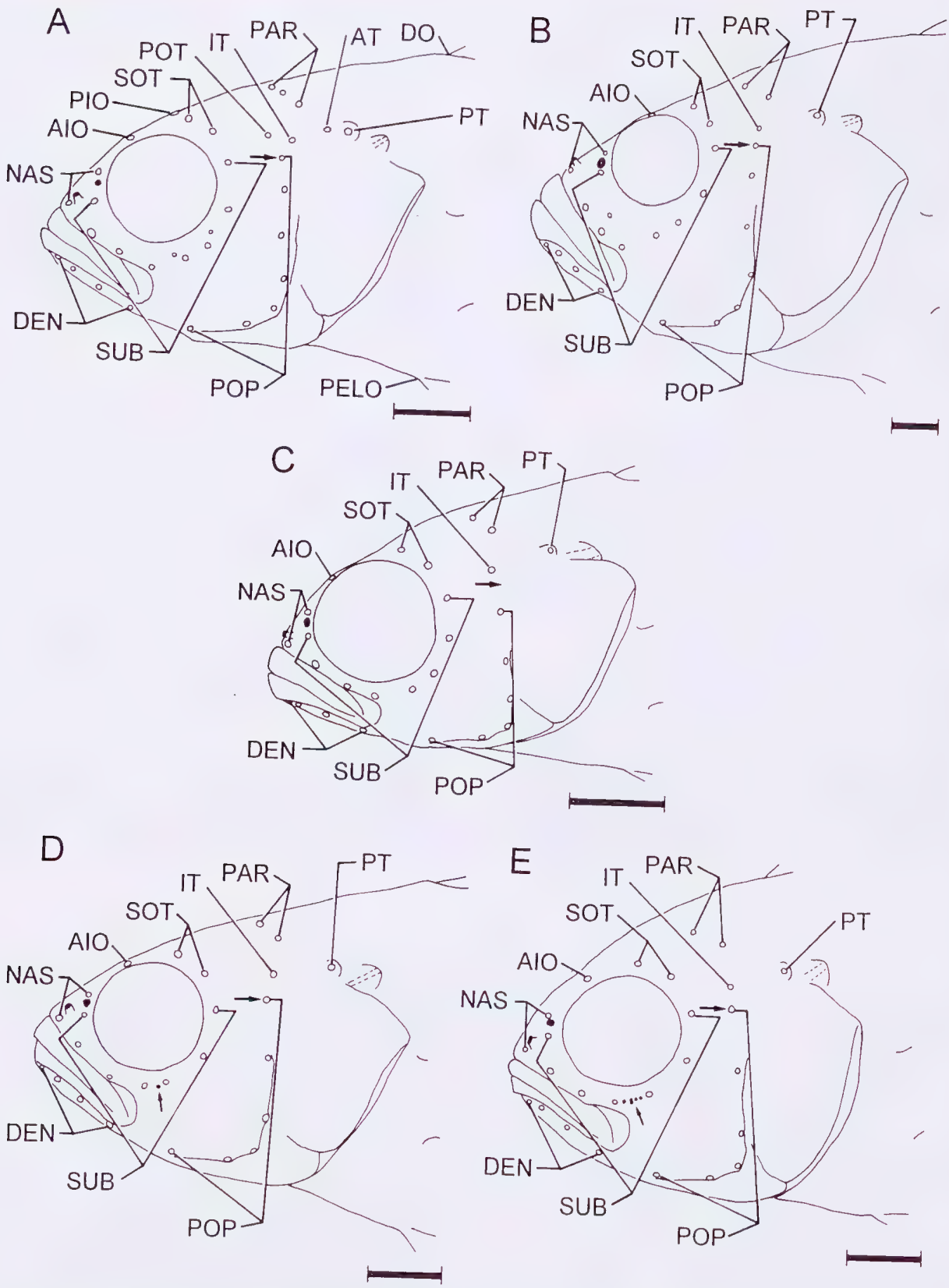

Figure 12. Left lateral diagrams of heads of selected pseudoplesiopine species: A, *Lubbockichthys multisquamatus*, AMS I.220779-175, 36.3 mm SL; B, *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL; C, *Amsichthys knighti*, NTM S.11384-018, 25.0 mm SL; D, *Chlidichthys johnvoelckeri*, ROM uncat., (field number RW 88-26), 36.2 mm SL; E, *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL (paratype). Large arrow indicates dorsal tip of preopercle. Superficial neuromasts in D and E shown in black and indicated by small arrow. Abbreviations: AIO, anterior interorbital pore; AT, anterior temporal pore; DEN, dentary pores; DO, dorsal-fin origin; IT, intertemporal pore; NA, nasal pores; PLO, pelvic-fin origin; PAR, parietal pores; PIO, posterior interorbital pore; POP, preopercular pores; POT, posterior otic pore; PT, posttemporal pore; SOB, suborbital pores; SOT, supraotic pores. Scale bars = 2 mm.

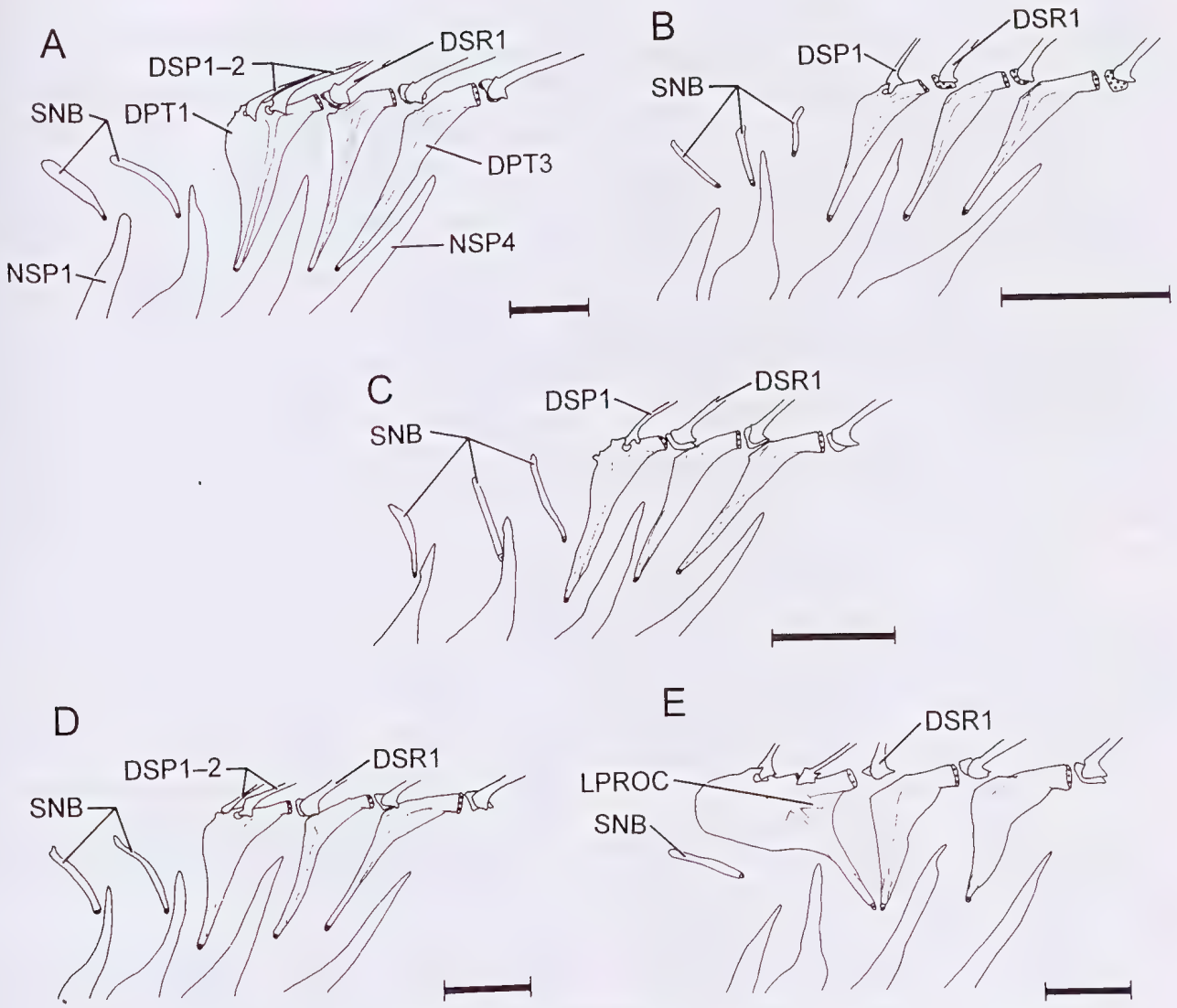

Figure 13. Anterior dorsal-fin pterygiophores and supraneural bones of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops howensis*, AMS I.19755-024, 21.0 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in large stipple. Abbreviations: DPT1,3, dorsal-fin pterygiophores 1,3; DSP1-2, dorsal-fin spines 1–2; DSR1, segmented dorsal-fin ray 1; LPROC, lateral process on first dorsal-fin pterygiophore; NSP1,4, neural spines 1,4; SNB, supraneural bones. Scale bars = 1 mm.

fin origin near the vertical through the preopercle (Figs. 5, 7E; state 1), a condition that we consider apomorphic.

Character 18. Single supraneural bone. Lubbockichthys, Pseudoplesiops, Amsichthys, Chlidichthys, Assiculoides, Assiculus and anisochromines have more than one supraneural bone (Fig. 13A–D; state 0). *Pectinochromis* has a single supraneural bone (Fig. 13E; state 1). Congrogadines have one to three tiny supraneural bones, varying considerably within species. We regard the single supraneural in *Pectinochromis* apomorphic.

Character 19. Numerous outer first-gill-arch rakers. Most pseudoplesiopines have relatively low to moderate numbers of total rakers on the outer face of the first gill arch: 12–16 for *Amsichthys*; 9–17 for *Pseudoplesiops*; 12–19 for *Chlidichthys*; and 12–21 for *Lubbockichthys* (state 0). The outgroup taxa have similar low to moderate numbers: 3–9 in anisochromines; 6–17 in congrogadines; 14–18 in *Assiculoides*; and 13–17 in *Assiculus*. *Pectinochromis* is distinctive in having numerous rakers on the outer face of the first arch, ranging from 27–31 (state 1). This state is regarded as apomorphic.

Character 20. Segmented pelvic-fin rays all unbranched. Adult specimens of *Lubbockichthys* have one or more segmented pelvic-fin rays branched (state 0). *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* have all segmented pelvic-fin rays unbranched, (state 1). With the exception of some congrogadines that lack pelvic fins, the outgroup taxa have one or more branched segmented rays in the pelvic fin. The absence of branched rays is therefore regarded as apomorphic.

Character 21. Posterior otic pores absent. Adult specimens of *Lubbockichthys* have one or more posterior otic pores on each side of the head (Fig. 12A; state 0). The remaining

pseudoplesiopine genera lack posterior otic pores (Fig. 12B–E; state 1). Posterior otic pores are present in *Assiculus, Assiculoides* and anisochromines, and are either present (*Halidesmus, Halimuraenoides* and *Congrogadus* (*Congrogadus*)) or absent (*Rusichthys, Haliophis, Natalichthys, Blennodesmus, Halimuraena* and *Congrogadus* (*Congrogadoides*)) in congrogadines (Winterbottom, 1986, 1996; Winterbottom & Randall, 1994). The lack of posterior otic pores is regarded as apomorphic within the Pseudoplesiopinae.

Character 22. Anterior temporal pores absent. Adult specimens of *Lubbockichthys* have an anterior temporal pore on each side of the head (Figs. 9A, 12A; state 0). The remaining pseudoplesiopine genera lack anterior temporal pores (Figs. 9B–E, 12B–E; state 1). *Assiculus, Assiculoides*, anisochromines and congrogadines possess anterior temporal pores; the absence of anterior temporal pores is therefore apomorphic within the Pseudoplesiopinae.

Character 23. Posterior interorbital pores. Adult specimens of *Lubbockichthys* have 1–2 (usually 1) median posterior interorbital pores on the head (Fig. 12A; state 0). The remaining pseudoplesiopine genera lack median posterior interorbital pores (Fig. 12B–E; state 1). *Assiculoides* and *Assiculus* lack median posterior interorbital pores. However, such pores are present in anisochromines and the majority of congrogadines. The polarity of this character within the Pseudoplesiopinae is, therefore, equivocal.

Character 24. Third supraneural bone well developed. The third supraneural bone is small or absent in *Lubbockichthys, Pectinochromis*, anisochromines, congrogadines, *Assiculoides, Assiculus* and all but one species of *Chlidichthys* (Fig. 13A,D,E; state 0). *Amsichthys* and all but a few relatively derived *Pseudoplesiops* species have the third supraneural bone well developed (Fig. 13B,C; state 1), a condition that we consider to be apomorphic. *Chlidichthys abruptus* is unique among pseudoplesiopines in exhibiting considerable intraspecific variation in this character; approximately one quarter of specimens examined lacked a third supraneural bone, whereas the remaining specimens had a weakly to well-developed third supraneural bone.

Character 25. Three epurals. Lubbockichthys, Amsichthys and *Pseudoplesiops* have two epurals (Fig. 14A–C; state 0), as do anisochromines, *Assiculoides* and basal congrogadines. *Chlidichthys* and *Pectinochromis* have three epurals (Fig. 14D,E; state 1). *Assiculus* and most of the remaining pseudochromines also have three epurals. [The exceptions, aside from *Assiculoides*, are members of the *Pseudochromis tapeinosoma* group (Gill & Allen, 1996), which have two epurals.] Taken in the context of the scheme of outgroup relationships proposed herein, the three-epural state is most parsimoniously interpreted as apomorphic among pseudoplesiopines.

Character 26. Infraorbital 2 reduced or absent. In *Lubbockichthys, Amsichthys* and *Pseudoplesiops*, the infraorbital branch of the cephalic lateral-line systems passes through an uninterrupted series of canals in the five infraorbital bones (Fig. 10A–C; state 0). In *Pectinochromis*, infraorbital 2 is reduced in size and lacks a lateral-line canal, so that the canal passing through infraorbital 1 (lachrymal) does not communicate with the posterior series of canals (Fig. 10E; state 1). Infraorbital 2 is absent in *Chlidichthys*, giving a total of only four infraorbitals, and the canal passing through infraorbital 1 usually (see below) does not communicate with the posterior series of canals (Fig. 10D; state 2). The only *Chlidichthys* species in which there is communication between the anterior and posterior portions of the infraorbital canal (i.e., between infraorbitals 1 and 3) are the three members of a derived clade within the genus, *C. cacatuoides, C. inornatus* and *C. rubiceps*; we consider the uninterrupted series of infraorbitals in these species secondarily derived, and non-homologous with the outgroup condition. The outgroup taxa usually have the infraorbital branch of the cephalic lateral-line system passing through an uninterrupted series of canals in four (congrogadine genus *Natalichthys*), five (*Assiculoides*, anisochromines and most congrogadines) or six (*Assiculus*) infraorbital bones. (The noteworthy exception is the congrogadine genus *Rusichthys*, where only infraorbital bone 1 is present, and it does not communicate with the remainder of the cephalic lateral-line system.) Within the Pseudoplesiopinae, the reduction (through loss of the canal) and loss of infraorbital 2 are here regarded as an ordered transformation series. The reduction or loss of the second infraorbital in *Pectinochromis* and *Chlidichthys* is associated with the absence of a suborbital laterosensory pore that is present at the posterior opening of the second infraorbital in the remaining pseudoplesiopine genera. Instead, one or a series of superficial neuromasts are present between the tips of the first and third infraorbitals (Fig. 12D,E).

Character 27. Laterosensory-canal-bearing bones weakly developed. The laterosensory-canal-bearing bones of *Lubbockichthys, Pseudoplesiops* and *Amsichthys* are relatively well ossified, usually with well-developed laminar edges (Figs. 9A–C, 10A–C; state 0), as they are in the outgroup taxa (at least in adult specimens). In contrast, those of *Chlidichthys* and *Pectinochromis* are relatively weakly ossified, often with slit-like openings extending along the bones, and without well-developed laminar edges (Figs. 9D,E, 10D,E; state 1). We consider the latter apomorphic within the Pseudoplesiopinae.

Character 28. Second preopercular pore absent. Lubbockichthys has 6–11, rarely 6 (six only in small specimens) and *Pseudoplesiops* has 6–8, rarely 6 or 8, preopercular pores, with the upper two pores relatively closely spaced (Fig. 12A,B; state 0). *Pectinochromis* and *Chlidichthys* usually have only six preopercular pores (occasional specimens of both genera may have seven pores on one or both sides, but the configuration of upper pores is the same as in specimens with six pores), with the upper pore well separated from the lower pores (Fig. 12D,E; state 1). The relatively low number of pores is here argued to have resulted from the loss of the homologue of the second pore of the seven-pored genera, which results in the upper two pores being well separated from each other. *Amsichthys* also usually has only six pores (Fig. 12C), but the arrangement is here argued to be non-homologous with that

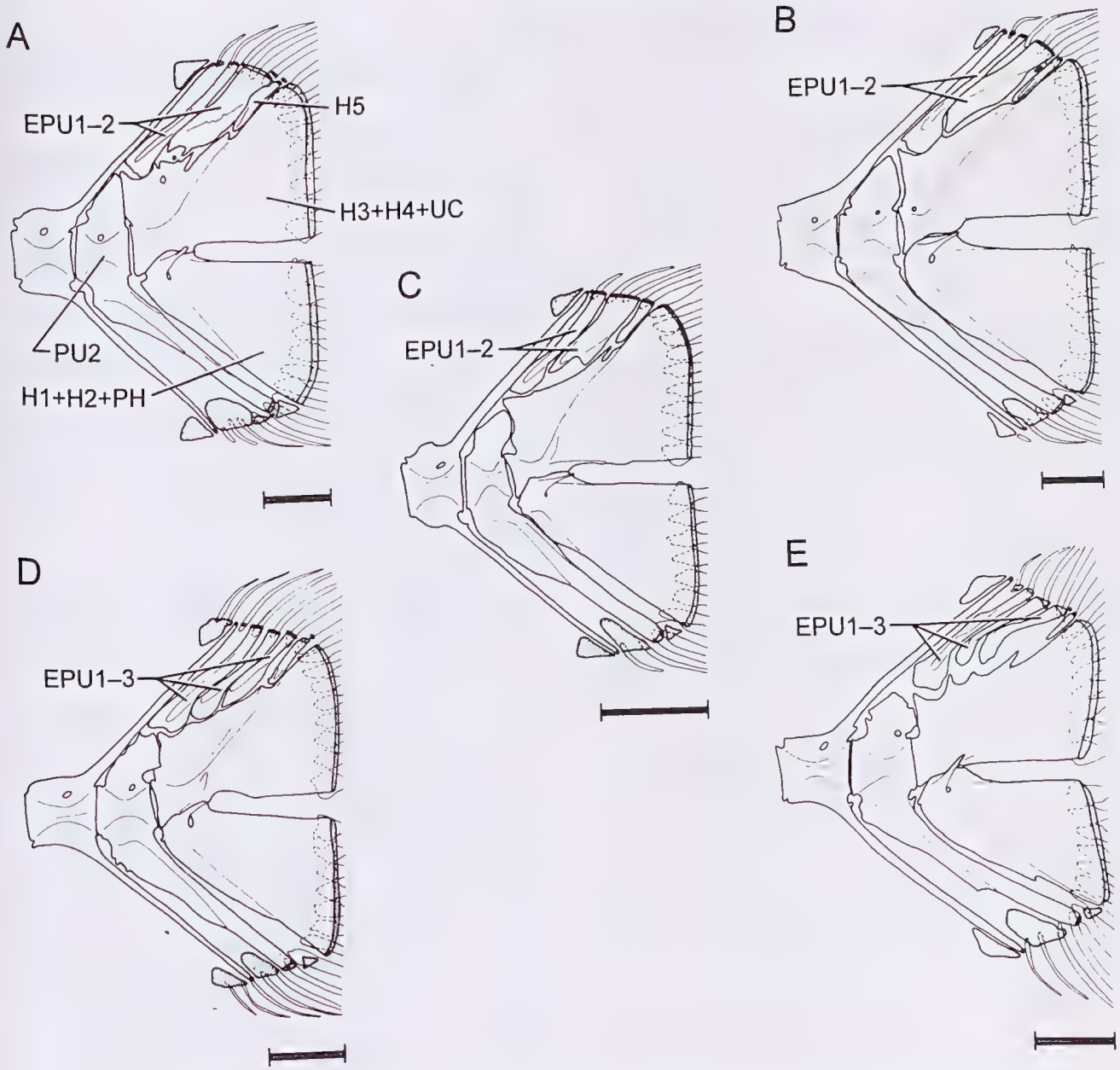

Figure 14. Caudal skeletons of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in dense stipple; overlapping portions of fin-ray bases shown in broken lines. Abbreviations: EPU1-3, epurals 1–3; H1+H2+PH, fused hypurals 1 and 2 and parhypural; H3+H4+UC, fused hypurals 3 and 4 and compound urostylar complex; H5, hypural 5; PU2, preural centrum 2. Scale bars = 1 mm.

of *Chlidichthys* and *Pectinochromis* (see Character 12 above). The outgroup taxa have the upper two preopercular pores relatively close together, and most have relatively high numbers of preopercular pores: 12–16 for anisochromines; 10–19 for *Assiculoides*; and 9–18 for *Assiculus*. Congrogadines usually have only six or seven preopercular pores (nine in the relatively derived species *Halidesmus polypterus*), but the upper two pores are not widely separated. Therefore, the condition shown in *Chlidichthys* and *Pectinochromis* is considered apomorphic within the Pseudoplesiopinae.

Character 29. Ten precaudal vertebrae. Lubbockichthys, Amsichthys and almost all *Pseudoplesiops* species have more than ten precaudal vertebrae (Table 2; state 0), as do most of the immediate outgroup taxa: 12–19 in congrogadines; 11–12 in *Assiculoides*; and 11 in *Assiculus*. *Chlidichthys* and *Pectinochromis* are unusual among pseudoplesiopines in having ten precaudal vertebrae (Table 2; state 1). Anisochromines, one relatively derived *Pseudoplesiops* species and most pseudochromines (the only exceptions are *Assiculoides, Assiculus* and *Labracinus*) also have ten precaudal vertebrae. However, parsimony dictates that the presence of ten precaudal vertebrae is apomorphic within the Pseudoplesiopinae.

Character 30. Eye large. Most pseudoplesiopines have relatively small eyes: 8.5–10.6% SL in *Chlidichthys*, 7.9–11.7% SL in *Lubbockichthys*, and 8.2–11.0% SL in *Pseudoplesiops* (state 0). *Pectinochromis* and *Amsichthys* are distinctive in having relatively large eyes, 10.5–11.9 and 9.9–12.5% SL, respectively (state 1); overlap with smaller-eyed taxa can largely be attributed to ontogenetic variation (smaller specimens have proportionally larger eyes). Outgroup taxa have relatively small to moderate eyes; the condition shown by *Amsichthys* and *Pectinochromis* is therefore considered apomorphic.

Character 31. Dorsal-fin-ray branching. Pseudoplesiops, Amsichthys and *Chlidichthys* have mostly simple (unbranched) segmented dorsal-fin rays (state 0). *Lubbockichthys* and *Pectinochromis* have mostly branched segmented dorsal-fin rays (state 1). The first outgroup has mostly branched rays in this fin, whereas the second and third outgroups have mostly simple rays in the dorsal fin. Polarisation of this character is therefore equivocal within the Pseudoplesiopinae.

Character 32. Segmented anal-fin rays mostly simple. Lubbockichthys and *Pectinochromis* have mostly branched segmented anal-fin rays, as do the outgroup taxa (state 0). Conversely, the remaining pseudoplesiopine genera have mostly simple segmented anal-fin rays (state 1). The latter condition is therefore apomorphic within the subfamily.

Results of Parsimony Analysis. Phylogenetic analysis of the 32 characters (Table 1) resulted in the single tree shown in Fig. 15: tree length = 36; consistency index = 0.91; retention index = 0.76. [A second analysis was also performed using only characters 20–32, with character 26 recoded as "1" for *Chlidichthys*. In so doing, untested characters (synapomorphies of the Pseudoplesiopinae, and unique, unequivocal generic autapomorphies) were excluded. The analysis yielded the same tree, with the following statistics: tree length = 16; consistency index = 0.81; retention index = 0.76.].

Characters supporting monophyly of the Pseudoplesiopinae and its genera are discussed above in the diagnoses for the respective taxa.

Three synapomorphies support monophyly of a clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops*: segmented pelvic-fin rays all unbranched (character 20); posterior otic pores absent (character 21); and anterior temporal pores absent (character 22). One additional character, posterior interorbital pores (character 23), either supports monophyly of the clade (state 1), or is an autapomorphy of *Lubbockichthys* (state 0); the equivocal nature results from the presence of both states in the outgroup taxa (state 0 in the first outgroup, state 1 in the second and third outgroups), and the basal position of *Lubbockichthys* within the Pseudoplesiopinae. Similarly, mostly unbranched anal-fin rays (character 32) and mostly unbranched dorsal-fin rays (character 31), provide equivocal support for the clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* (see below).

A single synapomorphy supports a sister-group relationship between *Amsichthys* and *Pseudoplesiops*: third supraneural bone well developed (character 24). However, as this character varies within *Pseudoplesiops*, and is intraspecifically variable in *C. abruptus*, support for this relationship is weak. The distribution of one other character, segmented anal-fin rays mostly simple (character 32), is equivocal; it either supports monophyly of *Amsichthys* + *Pseudoplesiops* (and occurs homoplastically in *Chlidichthys*), or diagnoses the more general clade that also includes *Chlidichthys* and *Pectinochromis*, with autapomorphic reversal in the latter genus. Mostly unbranched dorsal-fin rays (character 31) provides similar equivocal support for a sister relationship between *Amsichthys* and *Pseudoplesiops* (see below).

Five synapomorphies support a sister-group relationship between the Indian Ocean taxa *Chlidichthys* and *Pectinochromis*: three epurals (character 25); infraorbital 2 reduced or absent (character 26); laterosensory-canal-bearing bones weakly developed (character 27); second preopercular pores absent (character 28); and ten precaudal vertebrae (character 29).

Character 30—eyes large—is most parsimoniously interpreted as independently derived autapomorphies of *Pectinochromis* and *Amsichthys*.

The presence of mostly unbranched segmented dorsal-fin rays (character 31) has been cited as an autapomorphy of the Pseudoplesiopinae (Smith, 1954; Springer *et al.*,

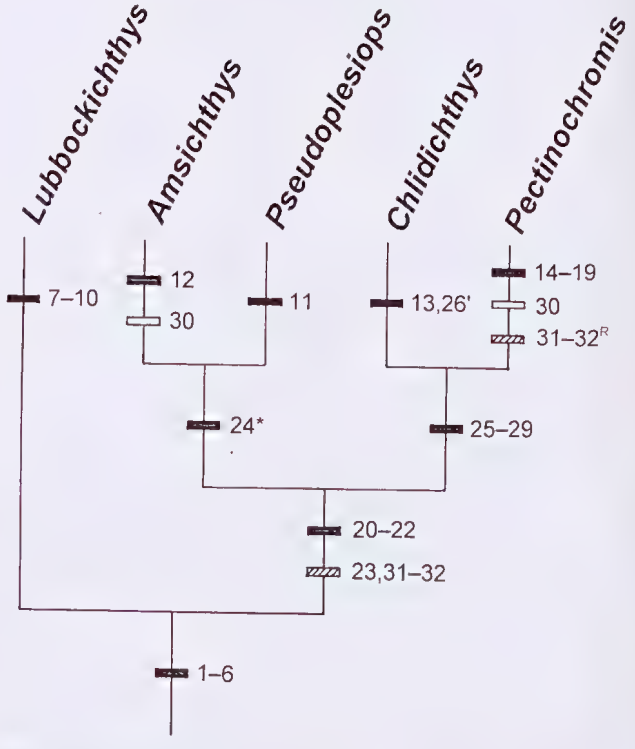

Figure 15. Cladogram of relationships between pseudoplesiopine genera generated from matrix in Table 1. Numbers indicate characters that support relationships (see text for details): solid bars indicate uncontradicted synapomorphies; open bars indicate homoplastic characters with unequivocal optimisations; hatched bars indicate homoplastic characters with equivocal distributions (see text for alternative optimisations); R indicates characters that reverse; * indicates characters that reverse within some derived (non-basal) species in terminal taxa; ' indicates derived state of multistate character.

Table 2. Comparison of selected characters of pseudoplesiopine genera. * Anterior extent of predorsal scalation is expressed in terms of proximity of anterior edge of first scale to either interorbital or supratemporal laterosensory commissure.

genus	dorsal-fin rays	anal-fin rays	pectoral-fin rays	pelvic-fin rays	total caudal-fin rays	vertebrae	anterior extent of predorsal scalation*	scales in lateral series
Amsichthys	I,23–24	I–II,13–15	16–18	I,4	24–25	11 + 18	interorbital	30–33
Chlidichthys	II,21–24	II–III,12–15	16–19	I,4	25–29	10 + 17–19	supratemporal to interorbital	37–52
Lubbockichthys	II,24–26	II,14–16	16–19	I,4	24–27	12–14 + 17–19 = 30–32	supratemporal	51–66
Pectinochromis	II,22–23	II,12–13	16–17	I,4	22–24	10 + 16–17	interorbital	35–39
Pseudoplesiops	I–II,22–29	I–III,13–18	15–18	I,3–4	23–26	10–14 + 17–21 = 28–33	supratemporal to interorbital	26–42

1977; Godkin & Winterbottom, 1985). However, the present analysis reveals that this character is homoplastic, with both character states occurring within the subfamily and its immediate outgroups. There are three equally parsimonious optimisations of the character, none of which provides support for monophyly of the Pseudoplesiopinae: (1) rays mostly branched (state 1) a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with reversal to mostly unbranched rays (state 0) in the clade consisting of *Amsichthys, Chlidichthys, Pectinochromis* and *Pseudoplesiops*, and autapomorphic acquisition of mostly branched rays in *Pectinochromis* (accelerated transformation optimisation); (2) independent acquisition of branched rays in Anisochrominae + Congrogadinae, *Lubbockichthys* and *Pectinochromis* (delayed transformation optimisation); and (3) mostly branched rays a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with independent reversal to mostly unbranched rays in *Chlidichthys* and in the clade consisting of *Pseudoplesiops* and *Amsichthys*.

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A New Species of *Graphium* Scopoli (Lepidoptera: Papilionidae) from the Bismarck Archipelago, Papua New Guinea

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ABSTRACT. *Graphium kosii* n.sp., a butterfly from high elevations in southern New Ireland, is described and figured. A key is presented for this and five closely related species: *Graphium weiskei* (Ribbe), *G. stresemanni* (Rothschild), *G. batjanensis* Okano, *G. macleayanum* (Leach) and *G. gelon* (Boisduval), all of which are confined to the Australasian region.

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This paper is the first of two treating new butterflies from little known montane forests of New Ireland. It describes a new species of *Graphium*. New Ireland is a long (c. 400 km) ancient island arc situated northeast of New Britain (2°–4°S 151°–153°E). The highest land reaches 2399 m in the southern "Lak" district and represents eroded, andesitic volcanoes, approximately 25 million years old (Pigram *et al.*, 1990). The biomes here are vertically diverse with lowland rainforest, mid and upper montane moss forest and a high montane heath vegetation, shown in Fig. 1 (McCallum & Sekhran, 1997). The International Conservation and Development Organisation (ICAD) attempted to procure the land proximal to the Weiten Rift Valley as World Heritage during 1992–1996 but terminated the project due to "land ownership difficulties" (P. Lavender, Pacific Heritage Foundation, pers. comm., 1998).

The "*weiskei*" group of butterflies within the genus *Graphium* comprises six closely related species: *G. macleayanum, G. weiskei, G. batjanensis, G. stresemanni, G. gelon* and the new species described here, *G. kosii* n.sp. All the species are restricted to the Australasian region, generally in and adjacent to mountainous areas. Saigusa *et al.*, (1977) showed more general phylogenetic relationships of this group with *G. empedovana* (Corbet), *G. codrus* (Cramer), *G. sarpedon* (Linnaeus), and *G. cloanthus* (Westwood).

Graphium macleayanum occurs as four subspecies in eastern mainland Australia, Tasmania, and Lord Howe Island (Common & Waterhouse, 1981) and in highland Papua New Guinea (Sands & Fenner, 1978). The various subspecies differ generally in the extent of the green in the basal area on the forewing above. Specimens from Mount Ginini (Australian Capital Territory) are distinct from most others from southeastern Australia in that they are small (forewing c. 29 mm) with broad wings, stunted tails and extensive greenish colouring. In this respect they more closely resemble specimens of *G. m. moggana* Couchman from Tasmania.

Graphium weiskei is a striking, well-known butterfly represented by the nominotypical subspecies and *G. w. goodenovii* (Rothschild), in upland mainland New Guinea and Goodenough Island, respectively (Parsons, 1998). Niculescu (1977) raised a monotypic genus, *Klinzigia*, for *G. weiskei* based primarily on its distinctive genitalia. However, he did not consider the other closely related species and, since then, this genus has been synonymised with *Graphium* (e.g., Hancock, 1983; Parsons, 1998). Haugum & Samson (1981) retained this as a subgenus for the whole "*weiskei*" group. Parsons (1998) recognised five main male colour forms from a study of many *G. weiskei* specimens from eastern Papua New Guinea.

Graphium batjanensis was described by Okano (1984) from an unknown locality in Batjan Island, Moluccas, but "it would be undoubtedly in the mountain area of 1,000 m high in Batjan Is." (Okano, 1984). This species is fairly common in the high mountains of southern Batjan (A. Lambartan, pers. comm.). Hancock (1985) treated this as a distinct species, although Parsons (1998) considered it conspecific with *G. weiskei*. The specific status of *G. batjanensis* is accepted in this work (see discussion). Parsons (1998) suggested that *G. weiskei* will eventually be discovered on Halmahera Island.

Graphium stresemanni was described by Rothschild (1915) from a series collected at Manusela, Central Seram (Ceram), above 1,000 m elevation, in 1912. Okano (1983) stated that the type locality was at "3250 ft". This species is distinct in bearing a full row of subterminal spots on the hindwing upperside, and by the shape of the male valva (see Fig. 3b).

Graphium gelon is superficially unrelated to the other species within the "*weiskei*" group, bearing a resemblance to other *Graphium* species—*G. sarpedon* and *G. monticolus* (Fruhstorfer). The genitalia of *G. gelon*, however, place it clearly within this group (Saigusa *et al.*, 1977). Okano (1984) illustrated the female genitalia and male valva of *G. gelon* but did not include those of the other species within the group. *Graphium gelon* is restricted to New Caledonia and the nearby Loyalty Islands (Holloway & Peters, 1976).

The new species, *Graphium kosii*, is so far only recorded from the high mountains of southern New Ireland, although it probably occurs on the Lelet Plateau, central New Ireland, where there has been a fleeting glimpse of "*G. weiskei* or a closely related species" (Parsons, 1998).

Materials and methods. This study was based on material borrowed from the following institutions.

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
BMNH	British Museum (Natural History), London
CJMC	private collection of C.J. Müller, Sydney
DHC	private collection of D. Hall, Sydney
EPC	private collection of Edward Petrie, Sydney
KONE	Department of Primary Industries, Konedobu, Papua New Guinea
RGC	private collection of R. Gotts, Winmalee, Australia
RMC	private collection of Russell Mayo, Newcastle, Australia
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden, Holland
SGC	private collection of S. Ginn, Sydney

Morphological terms and their abbreviations applied here conform with those used by Common & Waterhouse (1981).

Key to taxa within the "*weiskei*" species group of *Graphium*

1 Hindwing with tail at vein CuA1 vestigial/absent ..... *Graphium gelon* (Boisduval)

—— Hindwing with tail at vein CuA1 well developed 2

2 Forewing above with basal area beneath cell cream/light green 3

—— Forewing above with basal area beneath cell shade of blue, blue-green, turquoise, mauve, purple and/or pink 6

3 Forewing above with only anterior half of cell green ..... *G. macleayanum wilsoni* Couchman

—— Forewing above with cell entirely green 4

4 Beneath suffused yellowish ..... *G. macleayanum insulana* (Waterhouse)

—— Beneath not suffused yellowish 5

5 Forewing above with basal area green beyond cell towards dorsum ..... *G. macleayanum moggana* Couchman

—— Forewing above with basal area not green beyond cell . *G. macleayanum macleayanum* (Leach)

6 Hindwing vein M2 longer than forewing vein CuA2 7

—— Hindwing vein M2 shorter than forewing vein CuA2 8

7 Thoracic hairs ventrally light grey-brown ..... *G. batjanensis* Okano

—— Thoracic hairs ventrally pink ..... *G. kosii* n.sp.

8 Hindwing above with subterminal spots well developed ..... *G. stresemanni* (Rothschild)

—— Hindwing above with subterminal spots absent or vestigial 9

9 Hindwing subtornal spots either side of vein CuA1 with length similar to width ..... *G. weiskei weiskei* (Ribbe)

—— Hindwing subtornal spots either side of vein CuA1 with length much greater than width ..... *G. weiskei goodenovii* (Rothschild)

Figure 1. Hans Meyer Range southern New Ireland at 2300 m, c. 100 m below the summit—photograph of montane vegetation near the type locality.

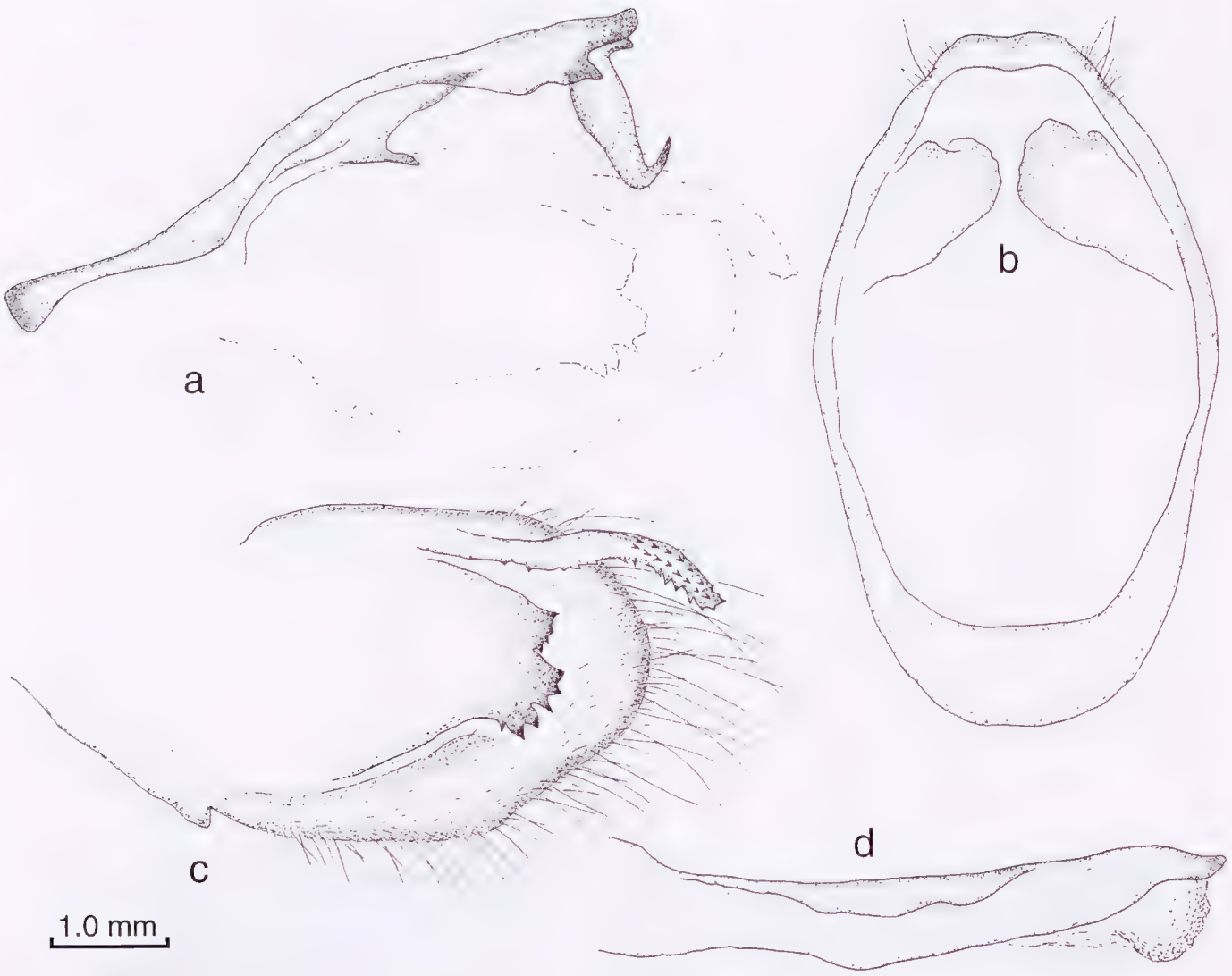


Figure 2. Male genitalia of *Graphium kosii* n.sp. (holotype ♂): a, lateral view; b, genitalic ring, dorsal view; c, left valva, lateral view; d, phallus, lateral view.

Graphium kosii n.sp.

Figs. 2a–d, 5–8

Type material. HOLOTYPE ♂, AM K111543, genitalia in vial attached to specimen in AM: "Lak district, Hans Meyer Range, 2400 m, S. New Ireland, 22 Aug. 1998, C.J. Müller". PARATYPES (44 ♂♂ and 5 ♀♀ all with same data as holotype unless otherwise indicated): 3 ♂♂ (one with genitalia dissected and attached to specimen) and 1 ♀ in ANIC; 3 ♂♂, 2 of which with genitalia dissected and attached to specimen and the third of which dated 20 August 1998, in BMNH; 3 ♂♂, 1 of which dated 20 August 1998 and 2 labelled "Lak district, Hans Meyer Ra., 1700 m, S. New Ireland, 18 Aug. 1998" in KONE; 3 ♂♂ (one with genitalia dissected and attached to specimen) in RNHL; 8 ♂♂ and 3 ♀♀, 4 of these 8 ♂♂ collected at an elevation at 1700 m and dated 18 August 1998 in CJMC; 15 ♂♂, 6 of which dated 20 August 1998, in DHC; 2 ♂♂ and 1 ♀ in SGC; 2 ♂♂ in RGC; 3 ♂♂, 1 of which dated 20 August 1998, in RMC; 2 ♂♂ in EPC.

Diagnosis. Forewing upperside basal and median markings brilliant turquoise, hindwings broad, ventral hairs on thorax and anterior segments of abdomen pink, genitalia with ring continuous, socii broad and simple, valva stepped.

Description. Male. (Figs. 5, 7). Head grey, covered with dense grey hairs above and pinkish-grey hairs beneath; antennae 19 mm long, brown, segmented deep brown-black, light brown ventrally, clubs broad and short, black dorsally and brown beneath; labial palpus, densely clothed with hairs, grey above, pinkish beneath. Thorax, densely haired, above grey-brown; beneath conspicuously greyish-pink; legs green. Abdomen, with thick hairs, deep grey-brown above and pinkish-brown beneath. Forewing 41.5 mm long, costa bowed strongly beyond postmedian area, termen straight between apex and vein M2, concave from vein M2 to CuA1, dorsum straight, above with ground colour black, a series of small, bluish-white submarginal spots from near costa to vein CuA2, congruent with termen except for proximal curve near apex; a large tear-shaped, dark green patch in postmedian area from, and normal to, costa to vein M2,

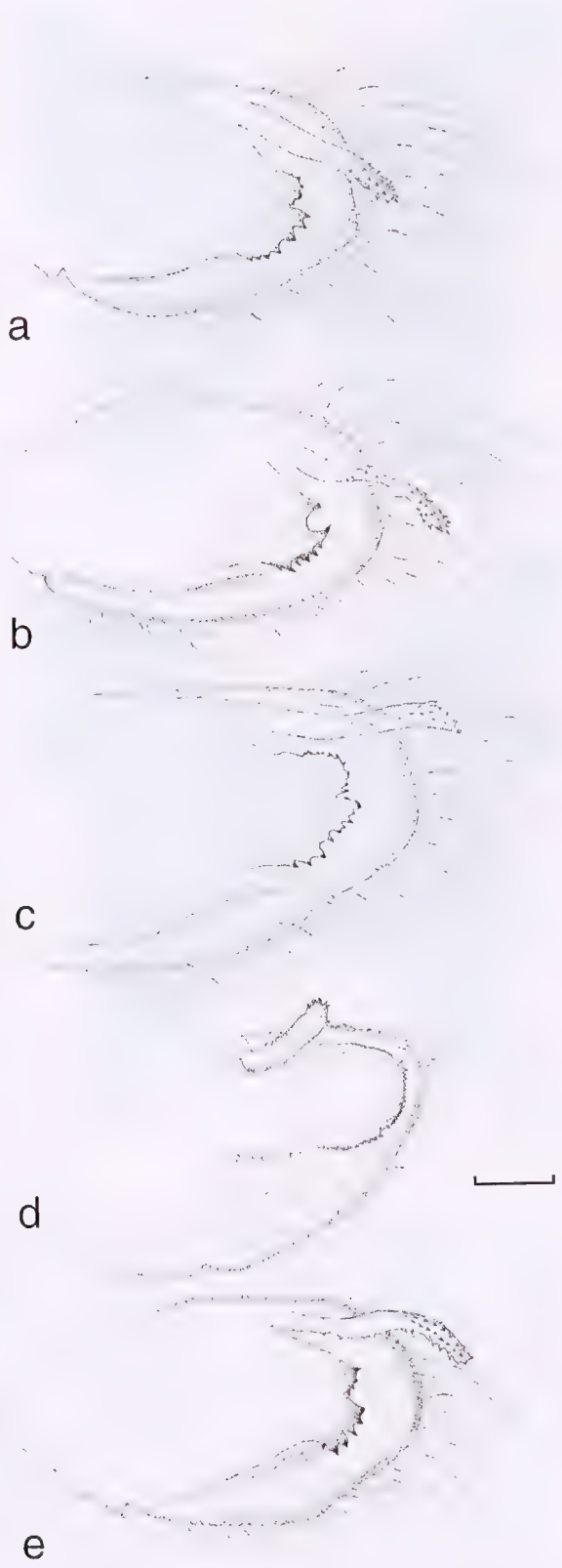


Figure 3. Lateral view of left valva. a, *G. weiskei* (Kerawagi, Papua New Guinea); b, *G. stresemanni* (Seram, Indonesia); c, *G. batjanensis* (Batjan, Indonesia); d, *G. macleayanum macleayanum* (Gosford, Australia); e, *G. kosii* n.sp. (New Ireland). Scale = 1.0 mm.

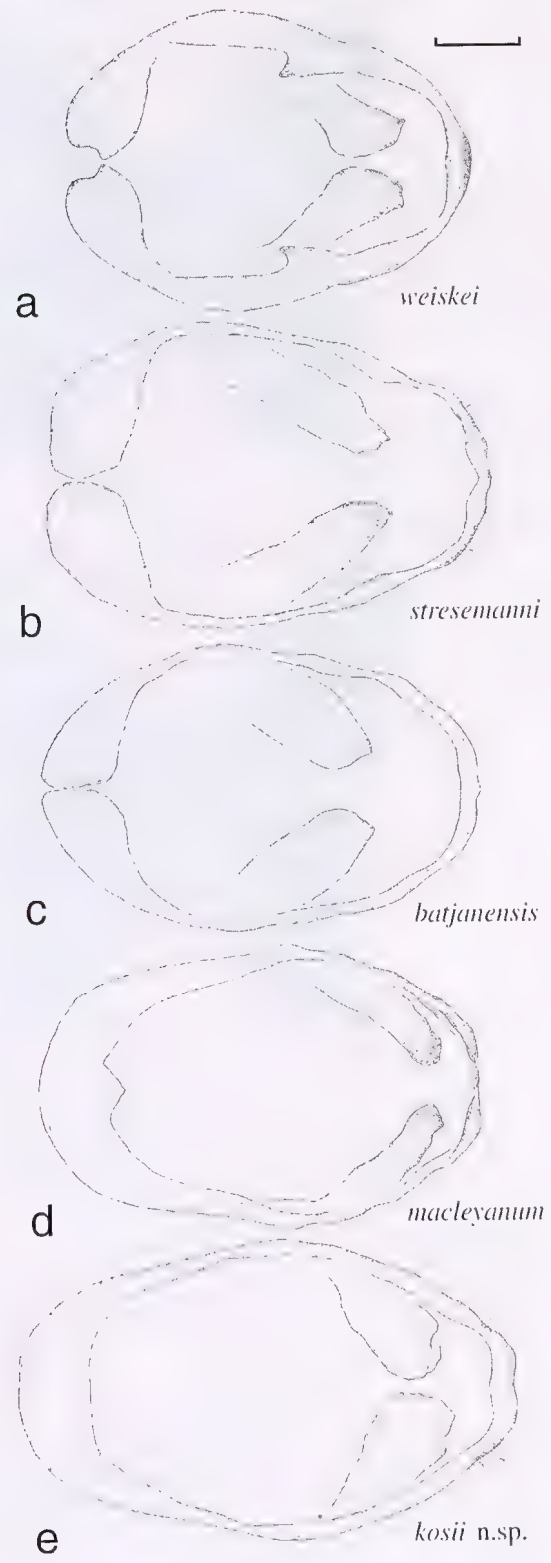
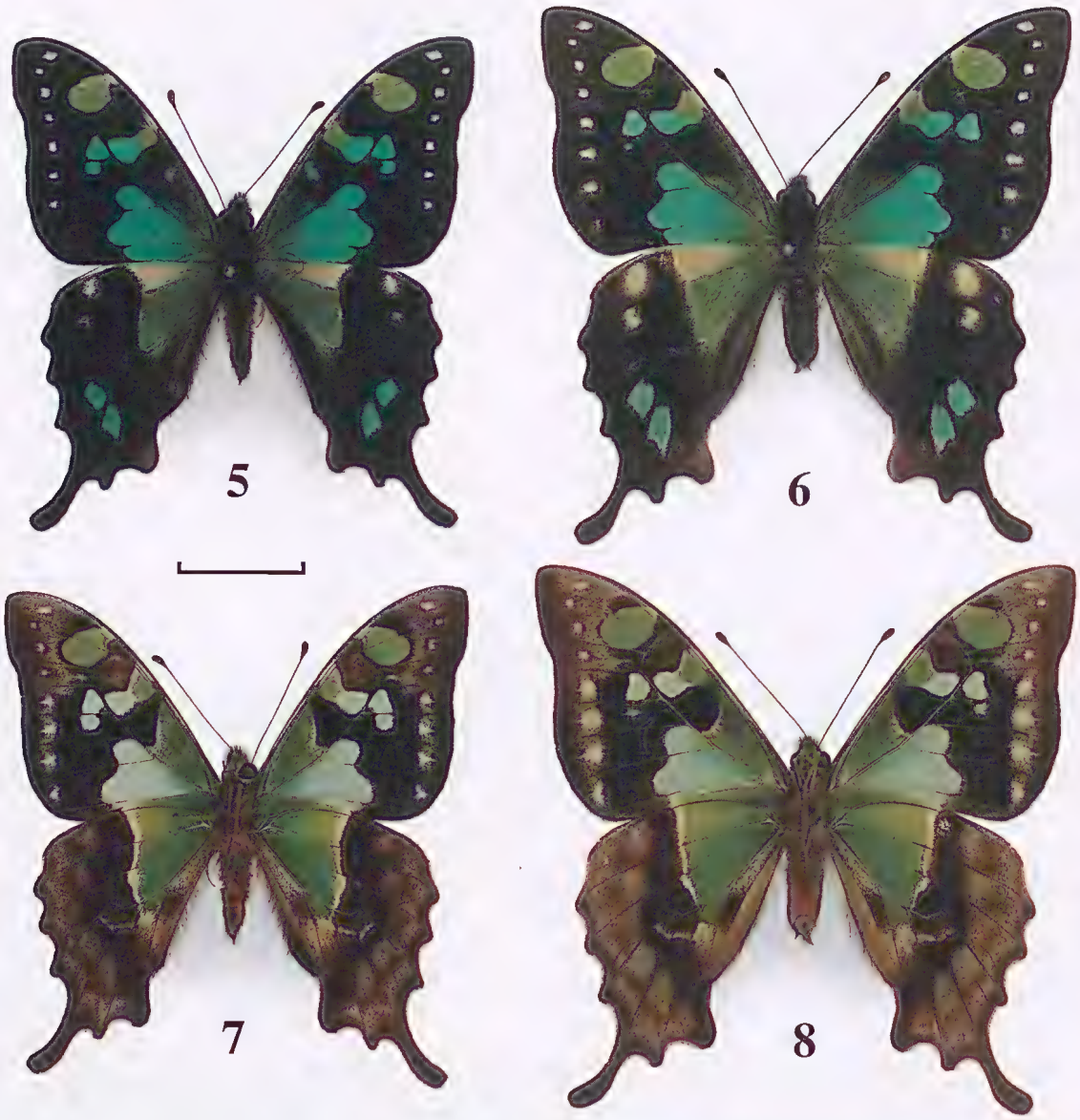


Figure 4. Dorsal view of male genitalic ring of *Graphium* species within the "*weiskei*" group, excluding *G. gelon*: a, *G. weiskei*; b, *G. stresemanni*; c, *G. batjanensis*; d, *G. macleayanum macleayanum*; e, *G. kosii* n.sp. Scale = 1.0 mm.



Figures 5–8. Adults of *Graphium kosii* n.sp. 3, holotype ♂ AM K111543, upperside; 4, paratype ♀ (CJMC), upperside; 5, holotype ♂, underside; 6, paratype ♀, underside. Scale = 20 mm.

intersecting veins white; a large "hour-glass" shaped marking in distal portion of cell approximately 1/5 distance from discocellulars to base, bright green in costal half and bright turquoise in remainder, two smaller turquoise spots in median area at end of cell to vein CuA1; a large basal turquoise area, below cell and vein CuA1, rounded distally between veins, basal portion of cell with obscure, deep green scales, often vestigial greenish-blue spot in middle of cell near costa, cilia narrowly black; beneath, ground colour brown in postmedian and apical area to vein M2, black in remainder, a series of small submarginal spots, greenish-white from apex to vein M2 and white and triangular in remainder, latter joined by scattered white scales; a postmedian patch near costa, shaped and coloured as above, median and basal pale markings shaped and positioned as in dorsal surface but bluish-white, costal half of "hour-glass" patch green; basal area with light blue scales below cell, large deep green area in cell, indented at lower half of cell in middle and tapered distally towards costa, white distal periphery, light brown scales in apical area tapering from costa to just beyond vein M3, cilia as above. Hindwing, narrow, with slightly spatulate tail at vein Cu A1, inner margin with fold supporting numerous dense grey sex hairs; lobed conspicuously at tornus, termen pronounced between veins; above ground colour black, deep green basal area from inner margin to junction of cell and veins Cu A2 and M2, concave at and white between vein Rs and costa, respectively; a small irregular white spot in apical area, vestigial blue spot beneath last spot; two turquoise tornal spots between veins M3 and Cu A2, well spaced, lower one larger and crescentic in shape, lobe chestnut brown, cilia pink or white; beneath, ground colour deep brown, darkening towards median area; a deep green basal area extending from bottom of cell and beyond, veins 1A+2A and Cu A2 and slightly bowed proximally to costa, narrowly crimson along costa at base and near apex; a white line of variable thickness separating basal area from brown distal 2/3 of hindwing; an acute, narrow white bar in median area

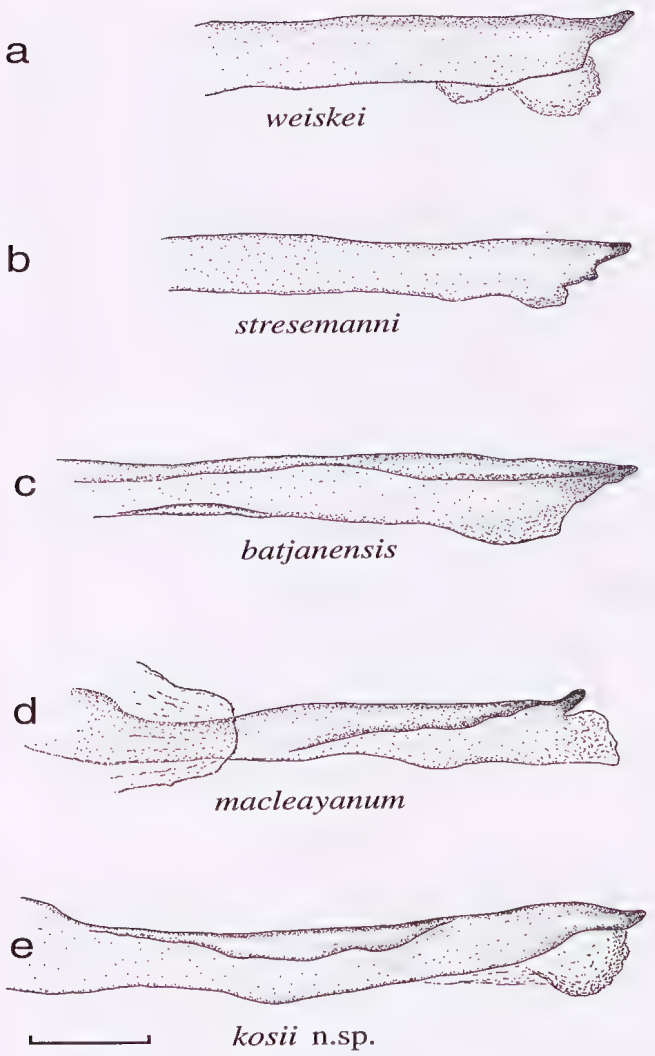


Figure 9. Lateral view of phallus of *Graphium* species within the "*weiskei*" group, excluding *G. gelon*: a, *G. weiskei*; b, *G. stresemanni*; c, *G. batjanensis*; d, *G. macleayanum macleayanum*; e, *G. kosii* n.sp. Scale = 1.0 mm.

between veins Cu A2 and M3, brownish-white scales between inner margin and cell, absent below junction of cell and vein 1A+2A, and also slightly bow-shaped brownish-white scales in submarginal area; vestigial bluish scales in tornal area identical in shape to tornal markings on upperside, cilia pink.

Female. (Figs. 6, 8). Similar to male but with both wings broader, submarginal spots in forewing much larger and whiter than in male, often extending to near dorsum; subapical white spots in hindwing upperside much larger and more obscure than in male, green and blue markings paler and slightly larger, postmedian spot below vein Cu A1 vestigial or absent; cell beneath with proximal green patch arcuate distally, submarginal markings beneath much paler than in male.

Male Genitalia. (Fig. 2). Genitalic ring long and continuous, oval-shaped, slightly concave anteriorly; socii broad; valva with ventrum straight, anteriorly toothed downward, aedeagus with anterior process.

Early stages. Unknown.

Measurements. Male forewing length 41.5 mm, antenna 19 mm; female forewing length 45 mm, antenna 21 mm.

Etymology. The new species name honours Tommy Kosi who, it is thought, collected the first specimens of this species.

Remarks. Only anecdotal information on Kosi's specimens can be found (L. Orsak, pers. comm., 1999). *Graphium kosii* n.sp. is the brightest species within the "*weiskei*" species group of *Graphium*. *Graphium kosii* may be readily separated from the other members of the species group by the colouration of the basal and median markings on the forewing above, which are deep turquoise, and by the broad hindwings which are only otherwise present in the Indonesian *G. batjanensis*. In addition, the hairs beneath the thorax and anterior segments of the abdomen are distinctly pink in *G. kosii*, a character developed elsewhere only in *G. macleayanum* and poorly in *G. weiskei*.

The genitalia of *G. kosii* provide useful diagnostic features in that the sociuncus ring is continuous and elongated posteriorly and the valva is distinctly stepped. Haugum & Samson (1981) recorded variability in the genitalia of *G. weiskei* but no such variability has been found among the five specimens of *G. kosii* examined, all of which fall outside the range of variation in the former species. The male genitalia of the other known species in the "*weiskei*" group are illustrated in Figs. 3–4.

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A New Species of *Cethosia* and a New Subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea

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ABSTRACT. Two butterflies *Cethosia vasalia* n.sp. (Nymphalidae) and *Delias messalina lizzae* n.subsp. (Pieridae) are described and figured from mid to high montane New Ireland. *Cethosia vasalia* n.sp. and *C. obscura* Guérin-Méneville are parapatric locally within the Bismarck Archipelago. These two species and their subspecies are compared in detail.

MÜLLER, C.J., 1999. A new species of *Cethosia* and a new subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea. *Records of the Australian Museum* 51(2): 169–177.

This paper is the second describing new butterflies from montane forests of New Ireland; geographic and locality information is given in the first (Müller & Tennent, 1999). The genus *Cethosia* Fabricius, which occurs from Sri Lanka and India, in the Andamans and Nicobars, through Southeast Asia to eastern Papua New Guinea and northern Queensland, is represented by about ten species. Parsons (1989b, 1998) provided keys to the New Guinean genera of Heliconiinae, one of which is *Cethosia*. A new species, *Cethosia vasalia* n.sp., is described here from New Ireland. It superficially resembles *C. obscura* Guérin-Méneville, which occurs generally throughout the Bismarck Archipelago and together, these species are the most melanic in the genus.

All stages of *Cethosia* species may be unpalatable to predators (see Parsons, 1998). Evidence of this is provided by the bright colouration of adults and larvae, the latter, where known, also being gregarious. Larvae of *Cethosia* are capable of moving very quickly and this may be a means of escaping from green tree ants (*Smaragdina* sp.) which frequent the fresh tips of their vine foodplants (Passifloraceae).

Butterflies belonging to the genus *Delias* Hübner are commonly known as "jezebels" and are popular with enthusiasts worldwide, owing to their generally bright ventral surfaces. To date there are 236 species described (G.J.M. Gerrits, pers. comm., 1998); the majority occur within mainland New Guinea where there appears to have been explosive speciation in the Tertiary, possibly due to a complex geological evolution of that island. Elsewhere, members of this genus are distributed from the Himalayas through Southeast Asia to New Guinea, Solomon Islands, Vanuatu, New Caledonia and Australia. Numerous taxa exist to the west of New Guinea, whilst in the Bismarck Archipelago eight species are recorded and in the Solomon Islands only four species (Arora, 1983).

Most larval foodplants recorded for *Delias* butterflies are mistletoes (Loranthaceae), although many remain undocumented. A revision by Talbot (1928–1937) remains the principal work on this genus. Talbot's primary division was based on androconial form and wing pattern similarities and an extensive key was presented.

Materials and methods. This study was based on material borrowed from the following institutions.

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
BPBM	Bernice P. Bishop Museum, Honolulu
BMNH	British Museum (Natural History), London
CJMC	private collection of C.J. Müller
GJMGC	private collection of Fred Gerrits, Buderim, Australia
RGC	private collection of Robert Gotts, Winmalee, Australia
SGC	private collection of S.G. Ginn, Sydney

Morphological terms and their abbreviations applied here conform with those used by Common & Waterhouse (1981).

Taxonomy

Cethosia vasalia n.sp.

Figs. 1, 2, 9, 10, 17–19, 23, 27, 29

Type material. HOLOTYPE ♂, "Schleinitz Mts., Central New Ireland, 990 m, 26 July 1998, C.J. Müller" AM K111544, genitalia dissected and attached to specimen. PARATYPES (5 ♂♂, 4 ♀♀): 1 ♂ same data as holotype, genitalia slide No. 13097, ANIC; 1 ♂ same data as holotype, genitalia dissected and attached to specimen, BMNH; 2 ♀♀ labelled "New Ireland, Lelet Plateau, 1000 m, 2 Oct–18 Dec, 1963, W.W. Brandt, Sir E. Hallstrom", ANIC; 1 ♀ "New Ireland, December 1923 (A.F. Eichhorn)", BMNH; 1 ♂ same data as holotype, SGC; 2 ♂♂ same data as holotype except dated 23 July 1998, CJMC; 1 ♀ labelled "Hans Meyer Ra., S. New Ireland, 2300 m, 22 Aug. 1998, C.J. Müller", CJMC.

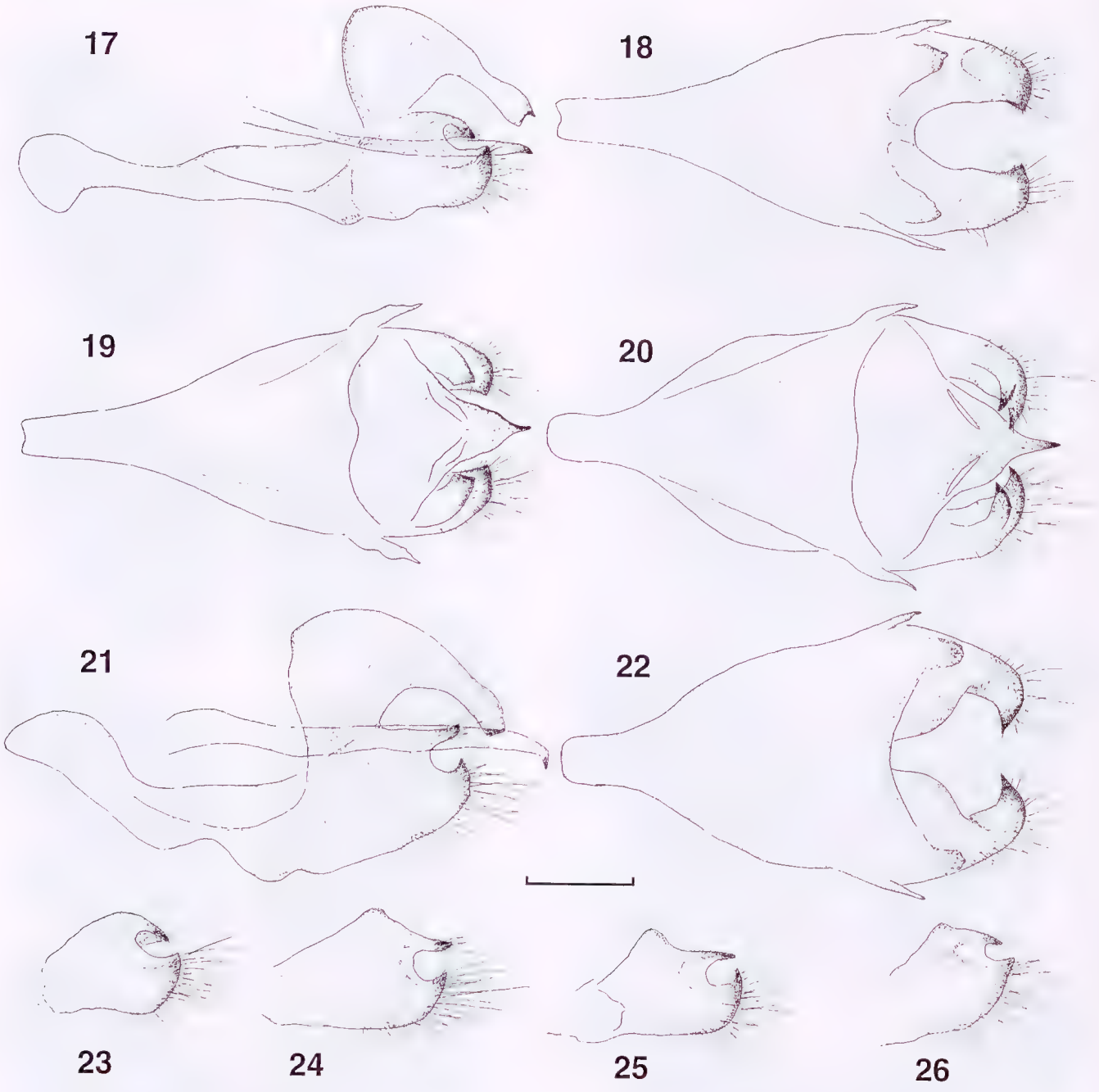
Diagnosis. Thorax and abdomen black. Mid-tibia with fine spines and narrow spurs, distally. Antennal clubs reaching well beyond discocellulars. Fore wings with four predominantly vestigial median to submarginal bands, pure white on upperside and extending conspicuously into hind wing as cusps, broken proximally toward the costa. Underside of hindwing, with mauve markings within the cell and between veins 1A+2A and Sc+R1, in median area. Genitalia with valvae closely spaced, sclerotised posterior hooks blunt and parallel, sociuncus anteriorly/laterally square-shaped with dorsoanterior process, strongly dipping, phallus blunt.

Description. Male. (Figs. 1, 2). Head black, with two pairs of white spots, adjacent to eye, dorsally and anteriorly; antennae long, black with deep brownish orange-tipped clubs, ventrally; labial palpus black with brown-black hair-tufts, beneath white, tending grey anteriorly. Thorax above black with fine brown-black hairs, beneath grey-black; legs deep grey, tending brown towards base, white posteriorly, mid-tibial spurs black, narrow. Abdomen black, beneath broadly segmented with white. Forewing with costa slightly bowed, termen conspicuously serrated between veins, slightly concave between veins M3 and tornus; above black with purple gloss from base to submarginal area; a series of white submarginal spots, cusp-shaped proximally, becoming vestigial towards apex; a band of irregularly shaped postmedian white spots, tending arcuate proximally towards costa; a pair of elongate white spots in postmedian and median area near costa; cilia broad, black at vein ends and white between; beneath with ground colour deep nut brown, basal area red, becoming orange near dorsum, forming an arcuate shape from inner margin about quarter of distance from tornus to distal part of cell to third distance along costa; a series of V-shaped white submarginal spots, becoming smaller towards apex; a further band of elongated, white postmedian spots, curving towards base near apex; two pairs of median spots between costa and vein Cu A1; vein M3 considerably bowed in median area beyond cell, inner row of white spots proximally bordered with elongate black spots, lowest reaching past vein Cu A1; two broad, irregular black bars either side of discocellulars, separated by grey-blue congruent but less extensive bars; two pairs of short, broad bars in upper one third of cell, each pair separated by grey-blue, short white bars between veins from termen to submarginal area; cilia as above. Hindwing, with termen indented between veins as in forewing, giving serrated appearance; above black with deep purple gloss from base to submarginal area; a series of crescent-shaped pure white submarginal spots, approximately congruent with termen, becoming smaller and divided towards costa; a restricted, subcostal purple-orange spot elongate between vein Rs and costa; inner margin grey; cilia as in dorsal surface of forewing; beneath, ground colour rich brown, deepening proximally; a series of white V-shaped submarginal markings, reaching to and slightly beyond row of irregular black markings in postmedian area, congruent with termen; a row of small black spots in median area, ringed narrowly with blue-grey, beyond bottom of cell only distally; a straight broad black bar near and normal to costa in median area; a series of three alternating pairs of black and blue-grey bars in basal area, basal of vein Sc+R1 black; a number of variable mauve spots in submedian area between veins 1A+2A and SC+R1; broad white bars reaching between veins from termen to submarginal area; cilia as above.

Female. (Figs. 9, 10). As in male but both wings broader with termen much more rounded; above with olive sheen replacing purple gloss in male; subcostal orange spot in hindwing very reduced and obscure; ground colour ventrally much greyer than in male; V-shaped markings with intracusp very dark and bisected by only narrow white lines, tapering basally; mauve median markings absent, replaced by broad black bars.

Figures 1–8. Adult males of *Cethosia* taxa from the Bismarck Archipelago. 1, *C. vasalia* n.sp., upperside (AM) (New Ireland); 2, *C. vasalia* n.sp., underside; 3, *C. obscura obscura* Guérin-Méneville, 1831, upperside (CJMC) (New Ireland); 4, *C. obscura obscura*, underside; 5, *C. obscura antippe* Grose-Smith & Kirby, 1889, upperside (CJMC) (New Britain); 6, *C. obscura antippe*, underside; 7, *C. obscura gabrielis* Rothschild, 1898, upperside (CJMC) (Manus Island); 8, *C. obscura gabrielis*, underside. Scale = 20 mm.

Figures 9–16. Adult females of *Cethosia* taxa from the Bismarck Archipelago. 9, *C. vasalia* n.sp., upperside (New Ireland); 10, *C. vasalia* n.sp., underside; 11, *C. obscura obscura*, upperside (New Ireland); 12; *C. obscura obscura*, underside; 13, *C. obscura antippe*, upperside (New Britain); 14, *C. obscura antippe*, underside; 15, *C. obscura gabrielis*, upperside (Manus Island); 16, *C. obscura gabrielis*, underside; all CJMC. Scale = 20 mm.



Figures 17–26. Male genitalia of *Cethosia* taxa from the Bismarck Archipelago. 17, *C. vasalia* n.sp., lateral view; 18, *C. vasalia* n.sp., ventral view; 19, *C. vasalia* n.sp., dorsal view; 20, *C. obscura obscura*, dorsal view; 21, *C. obscura obscura*, lateral view; 22, *C. obscura obscura*, ventral view; 23, *C. vasalia* n.sp., lateral view of right valva; 24, *C. obscura obscura*, lateral view of right valva; 25, *C. obscura antippe*, lateral view of right valva; 26, *C. obscura gabrielis*, lateral view of right valva. Scale = 1.0 mm.

Genitalia. (Figs. 17–19, 23). Uncus/tegumen rather narrow, uncus essentially square anteriorly but with sharp protrusion dorsally, dorsolateral flanges short and tapered, directed anteriorly, posteriorly concave in centre and bowed outwards dorsolaterally, laterally with deep, broad channels oval in shape; valva short and broad, sclerotised anteriorly with upper accessory dipping downward, dorsally parallel; vinculum saddle-shaped posteriorly; juxta short and blunt.

Early stages. Unknown.

Measurements. Male forewing length 44 mm, antenna 23 mm; female forewing length 48 mm, antenna 24 mm.

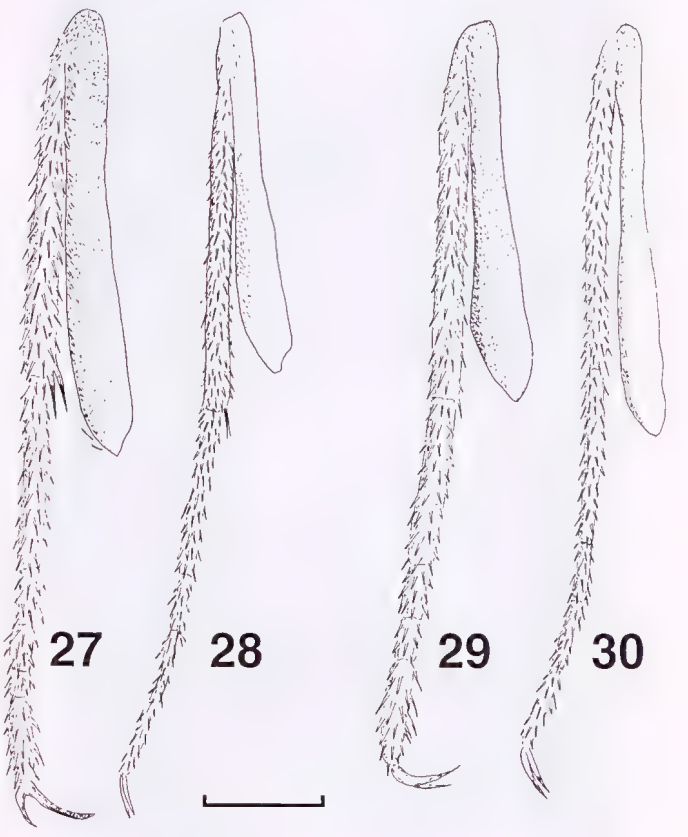
Remarks. *Cethosia vasalia* n.sp. is typical of the genus as shown by its characteristic terminal wing shape, serrated subterminal pattern on the underside of both wings and by the structure of the tarsal claws, which are long and simple (Figs. 27, 29) (see Parsons, 1998). The new species is superficially similar to *C. obscura* Guérin-Méneville (Figs.

3–8, 11–16, 20–22, 24–26, 28, 30), although displays several differences to that species. The antennae of *C. obscura* reach only barely beyond the distal part of the forewing cell whereas those of *C. vasalia* extend well past the discocellulars. The abdomen is orange-brown in *C. obscura* yet is always black in *C. vasalia*. Additionally, the legs in *C. vasalia* are much more robust and with well-developed tarsal spurs by comparison to *C. obscura* (Figs. 27–30). The patterns of both wings in *C. vasalia* are very distinctive, bearing four, mostly vestigial pure white, not dirty white to cream as in *C. obscura*, bands on both surfaces of the forewing and a costally bisected band on the hindwing, whilst in the various subspecies of *C. obscura*, only one well-developed band is present on both wings. Parsons (1998) figured a female from the W. Brandt collection held in ANIC (see Type material) as a "rare female form" of *C. obscura*. He separated this based on its pure white markings which are V-shaped and the overall dark appearance of the female. *Cethosia vasalia* is the darkest member of the genus. With no male material available until now, the species was considered a female form of the former species.

The male genitalia in the subspecies of *C. obscura* vary only slightly from one another in the shape of the valva (Figs. 24–26). In *C. vasalia*, the sociuncus apex is laterally square-shaped with a prominent upper spike, whilst in *C. obscura* it is saddle-shaped. The male valva in the latter species are widely spaced, unlike those in *C. vasalia* and possess long, tapering sclerotised hooks which are blunt and dorsally parallel in the new species. The vinculum is indented in *C. vasalia*, posteriorly, whilst in *C. obscura* it is rounded.

The parapatric distributions of *Cethosia vasalia* n.sp. and *C. obscura* Ribbe, on New Ireland is intriguing, considering the close affinities between the two taxa. Their occurrence in differing habitats with no obvious physical barriers has implications as to their possible evolution. Perhaps their separation may be postulated in a fashion similar to that for *Hypochrysops geminatus* Sands and its sister species, *H. pythias* (Lycaenidae) in mainland New Guinea. The former species does not occur below 1100 m although it is widely distributed on that island (Sands, 1986). *Hypochrysops pythias* is widespread in lowland regions from the Moluccas in eastern Indonesia to eastern mainland Papua and also in northern Queensland. Similarly, the highland species *C. vasalia* appears to exhibit a much more restricted distribution than the low altitude *C. obscura*, which occurs widely in the Bismarck Archipelago. Mainland New Guinea has experienced a structurally similar, although temporally distinct, geological evolution to that of New Ireland, the former being obducted above sea level fairly early in the Tertiary, c. 45 million years ago, whilst New Ireland became subaerial in the Miocene period, approximately 25 million years ago (Davies, 1990). Perhaps early influxes of each ancestral pair of species, here mentioned, became temporally isolated and fixed to the continual orogenesis, raising land in both islands. Subsequent waves possibly inhabited lower elevations and were adapted to different host plants at that stage. Sands (1986) records the larvae of *H. geminatus* on a *Commersonia* sp., different to the lowland and ubiquitous *C. bartramia* (L.) Merr., upon which the larvae of *H. pythias* feed (Common & Waterhouse, 1981; Sands, 1986). Parsons (1998) records *Adenia heterophylla* (Passifloraceae) as a host for *C. obscura* and the author observed females of *C. obscura* ovipositing on that plant at several locations in lowland New Ireland. Conversely, no plants of *A. heterophylla* were observed in the areas where *C. vasalia* was collected. It is possible that the larvae of *C. vasalia* feed on a species endemic to upland areas in New Ireland.

In central and southern New Ireland, *C. obscura* is not known to occur above approximately 500 m, while *C. vasalia* has been collected between 990 m and 2300m. South of Malum Village, central New Ireland, adults of both species were collected within 2 km of each other. *Cethosia o. obscura* is fairly common in lowland rainforest where it flies directly and quite rapidly, males within their territories often circle close to a vantage perch where they settle 2–6 m above the ground. Adults of *C. vasalia* were noted to fly rather more slowly than those of *C. obscura* and to settle frequently on the ground or on low vegetation. A further female specimen of *C. vasalia* was collected by the author in the Schleinitz Mountains at 990 m but was released, owing to its very poor condition.



Figures 27–30. Mid- and hind-legs of *C. vasalia* n.sp. and *C. obscura obscura*. 27, *C. vasalia* n.sp., mid-leg; 28, *C. obscura obscura*, mid-leg; 29, *C. vasalia* n.sp., hind-leg; 30, *C. obscura obscura*, hind-leg. Scale = 2.0 mm.

Delias messalina vigasa Parsons

Delias messalina naokomoritae Morita, 1995: 5, fig. 3, **n.syn.**

Delias messalina Arora, is a recently described species from the Solomon Islands. Arora (1983) described two subspecies, designating those from Bougainville (Papua New Guinea) as nominotypical; the other subspecies from Santa Isabel and Guadalcanal was named *orientalis*. Parsons (1989a) described *D. messalina vigasa* from eastern New Britain. *Delias m. naokomoritae* Morita, 1995 is clearly synonymous with *D. m. vigasa*. Both Parsons (1989a) and Morita (1995) described *D. m. vigasa* and *D. m. naokomoritae*, respectively, from two specimens. The holotype male of *vigasa* (BPBM) was used again for the description of *naokomoritae* and the names are therefore objective synonyms. Few specimens of *D. messalina* are known, in particular there are very few from the Bismarck Archipelago.

Arora (1983) suggested that *D. messalina* is closely related to *D. nigrina* (Fabricius) from eastern mainland Australia, although Parsons (1998) considered *D. messalina* to be more closely related to *D. weiskei* Ribbe from mainland New Guinea. Certainly, *D. nigrina* and *D. messalina* exhibit structural and behavioural similarities.

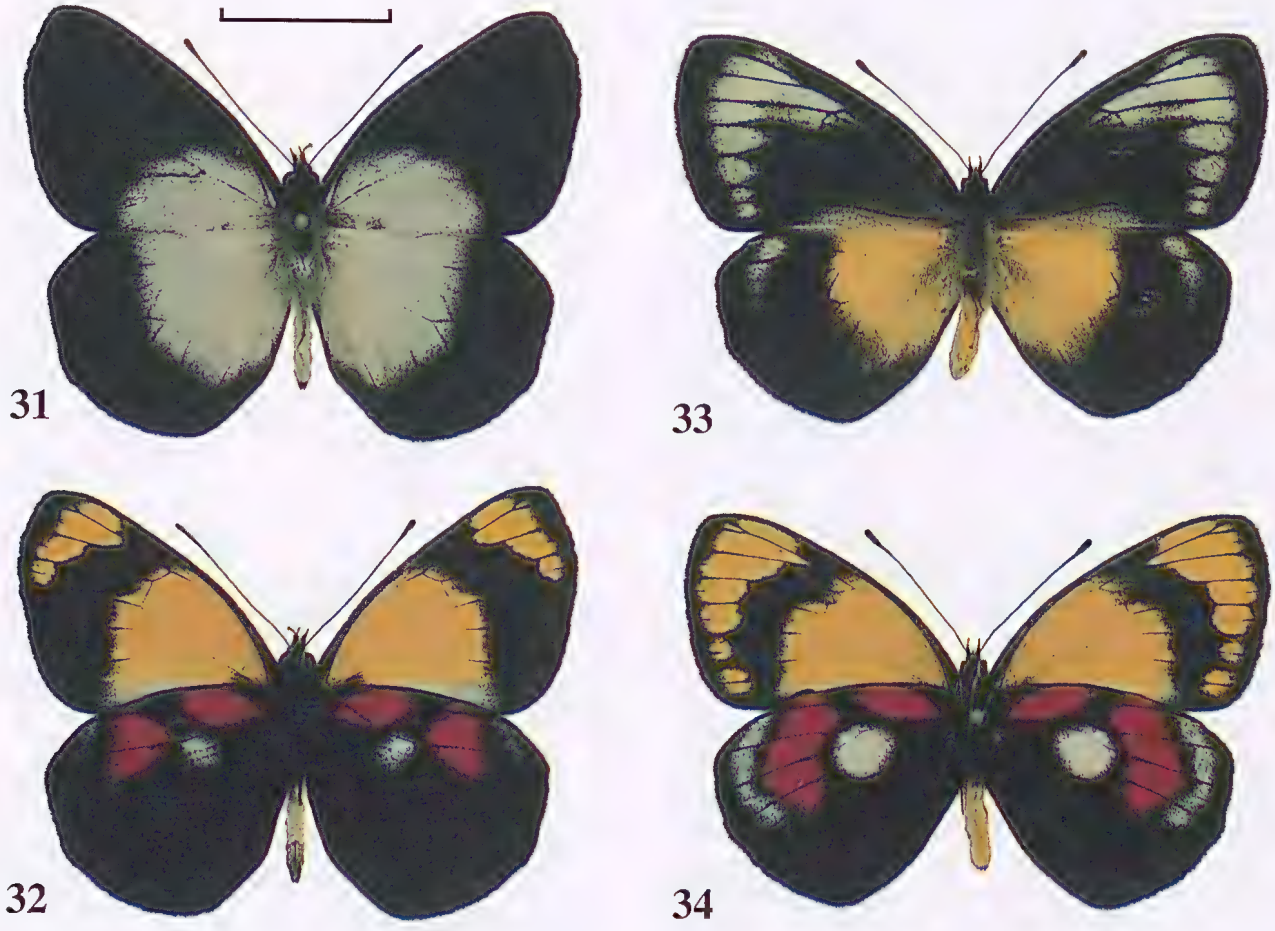
Delias messalina lizzae n.subsp.

Figs. 31–38

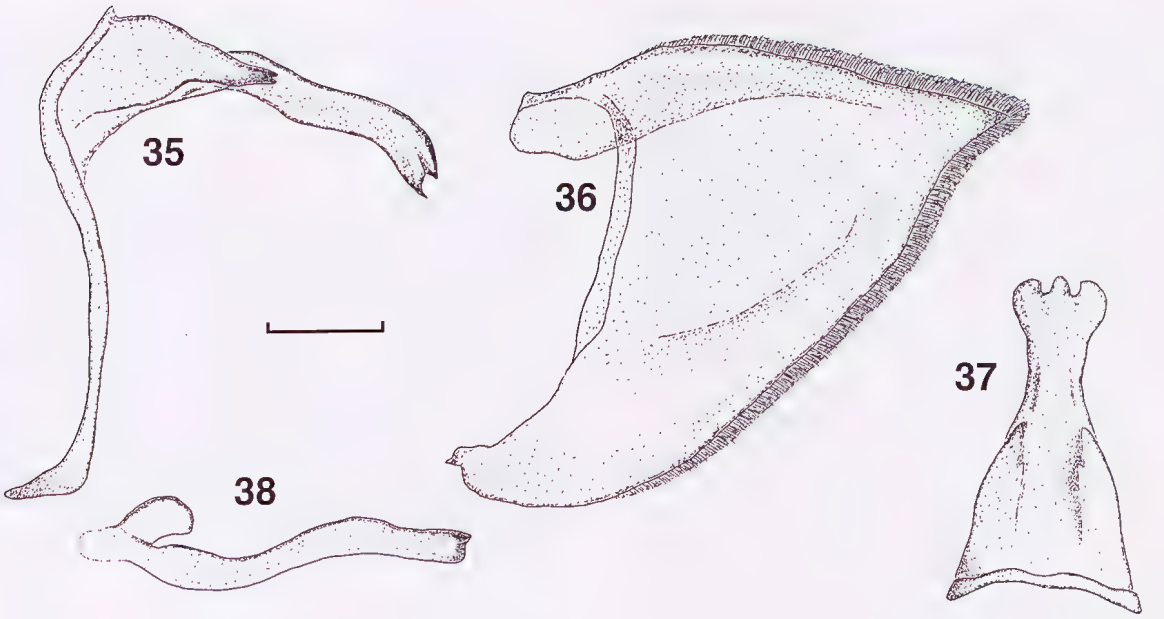
Type material. HOLOTYPE ♂, "Lak district, Hans Meyer Ra., S. New Ireland, 2400 m, 22 Aug. 1998, C.J. Müller" AM K111545, genitalia dissected and attached to specimen. PARATYPES: 5 ♀♀, all with same data as holotype, 1 in RGC, 2 in GJMGC and 2 in CJMC.

Diagnosis. Thorax beneath black. Abdomen white in male, yellow in female. Male fore and hind wings somewhat pronounced at veins M2 and apex, respectively, ground colour above with greenish sheen. Female with forewing submarginal band extending to dorsum on both surfaces and often reaching cell on upperside. Vestigial pale spots also present at apex of hindwing. Underside of hindwing in both sexes with scarlet markings very broad, circular spot in cell pure white. Genitalia with median lobe of uncus, dorsally spaced from lateral lobes which are flattened anteriorly, valva narrow, with ventrum nearly straight.

Description. Male. (Figs. 31, 32). Head black, clothed with dense deep grey hairs; labial palpus black, eye ringed with pale yellow anteriorly; antenna black, tipped white ventrally.



Figures 31–34. Adults of *Delias messalina lizzae* n.subsp. 31, holotype ♂, upperside; 32, holotype ♂, underside; 33, paratype ♀ (CJMC), upperside; 34, paratype ♀ (CJMC), underside. Scale = 20 mm.



Figures 35–38. Male genitalia of *Delias messalina lizzae* n.subsp. 35, lateral view of genitalic ring; 36, lateral view of left valva; 37, dorsal view of uncus; 38, lateral view of phallus. Scale = 0.5 mm.

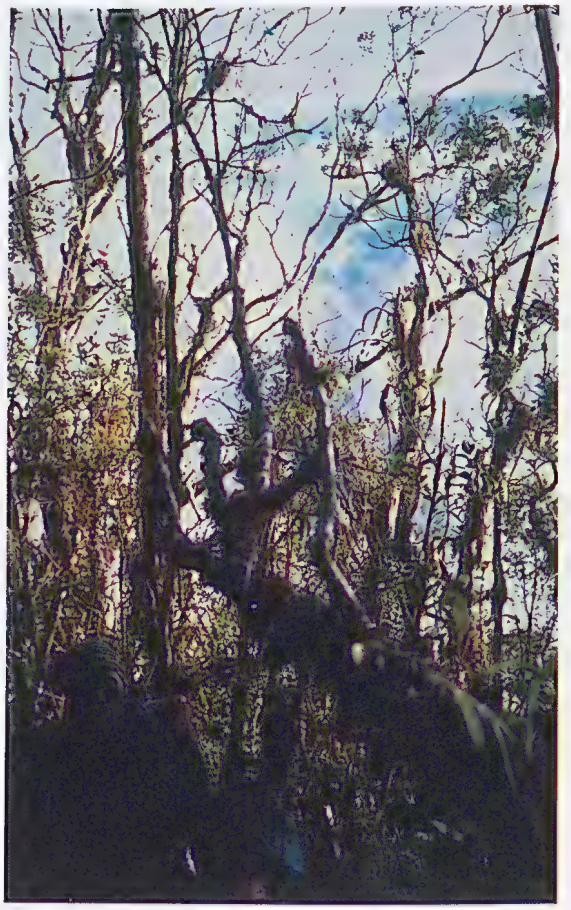


Figure 39. Hans Meyer Range, 2,000 m, southern New Ireland.

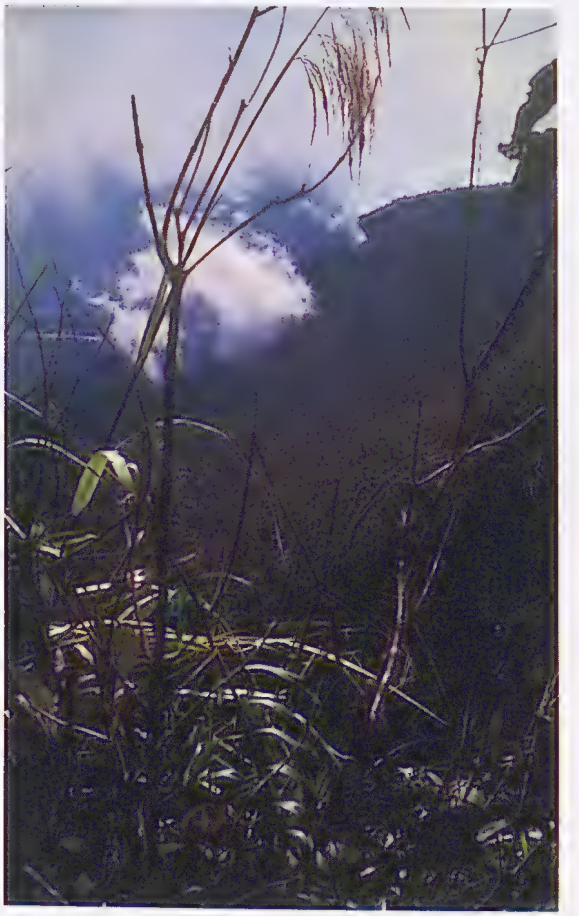


Figure 40. Hans Meyer Range, 1700 m, southern New Ireland.

Thorax black with long grey hairs dorsally, beneath black, legs black. Abdomen white, narrow black dorsal ridge, tapered posteriorly, claspers grey. Forewing with termen somewhat convex at vein M2; above with ground colour black with greenish sheen; basally light grey in an arcuate manner from approximately 1/8 along costa to junction of veins CuA1 and cell and to dorsum 1/4 of distance from apex; beneath black with bright yellow subapical band from costa to vein M3, vestigial between veins R3 and R4+5 and intruding abruptly between veins R3 and M2; base to postmedian area brilliant yellow, abruptly changing to white below vein 1A+2A; costa broadly black to vein Sc, black patch at base between cell and vein 1A+2A. Hindwing above with ground colours in dorsal surface of forewing; a large basal to median/postmedian light grey area extending from costa near apex to end of cell and to dorsum, about 2/3 of distance towards tornus, congruent with termen; beneath with ground colour black, an irregular small pure white spot in cell, approximately 2/3 distally; a large basal scarlet patch extending to vein Rs, rounded distally; a scattering of scarlet scales between veins Rs and M1; one vestigial and two large scarlet markings in median area between costa and M2, becoming irregular distally; a vestigial band of light grey scales near apex between veins Rs and M1.

Female. (Figs. 33, 34). Head, antennae, legs and labial palpus as in male. Thorax grey with dense yellow-grey hairs; beneath black. Abdomen yellow, with narrow black dorsal line, tapering posteriorly, beneath cream. Forewing, with costa and termen slightly bowed; dorsum straight; black above with deep greenish basal area, progressively becoming light grey and extending to postmedian area at dorsum; a well-developed series of white submarginal spots, elongate, especially between veins R4+5 and M3 and reaching into cell between veins M1 and M2, vestigial between veins R3 and costa, rounded distally; beneath black with pure white, circular spot in cell and reaching beyond intersections of veins Rs and M1; a large scarlet basal spot above cell and reaching vein Rs, a broad, conspicuous band of scarlet spots between costa and M3, in postmedian area; a band of silvery-grey markings from Sc+R1 to M3, elongate, approximately congruent with termen but running obliquely towards dorsum.

Genitalia. (Figs. 35–38). Uncus dorsally with median lobe separated from lateral lobes which are straight anteriorly, laterally with lower lobe downward dipping and tapered to a sharp point; valva fairly narrow and tapered to apex, ventrum nearly straight; ring concave ventrolaterally; juxta irregular and tapered ventrally.

Early stages. Unknown.

Measurements. Male forewing length 32 mm, antenna 17 mm; female forewing length 33 mm, antenna 18 mm.

Remarks. *Delias messalina lizzae* is a most striking member of the large genus *Delias* Hübner. The male of *D. m. lizzae* may be separated from those of other subspecies particularly by its rather acute wing shape and greenish gloss on the upperside of both wings. In addition, the pale basal area in both wings above is far more restricted than in other subspecies and is greyish in colour. Beneath, the hindwing bears large, bright red markings that are confined between the costa and vein M1. The male most closely resembles that of *D. m. vigasa* Parsons, ventrally, The female above is superficially most similar to *D. m. orientalis* Arora, although the white submarginal markings in the forewing of the former are very extensive and there is a greenish basal area. The hindwing above is bright yellow in the basal to median area and the subterminal spots near the apex are well developed. Beneath, the submarginal spots on the forewing are large and extend to the dorsum. The hindwing beneath bears a large pure white spot in the cell and the scarlet basal and median spots are very large.

The male genitalia of the new taxon are closer to *D. nigrina* than to the other subspecies of *D. messalina*, although the wing pattern is closer to *D. messalina*. In particular, the median lobe of the uncus is well separated from the lateral lobes and the valvae are much narrower with an almost straight ventrum.

Both sexes of the new taxon were observed and/or collected between 1400 m and 2400 m elevation, in the Hans Meyer Range, southern New Ireland. The biome here is one of high montane moss forest (Figs. 39, 40) and heathland, the latter is apparently peculiar to the upper peaks and ridges. Specimens of *D. m. lizzae* were collected above the canopy as they sailed with prevalent wind and were observed to fly as high as 60 m above the ground. Two females were observed flying high in the canopy (c. 30 m) at 1400 m apparently in search of oviposition sites. The type series of *D. m. vigasa* were collected between 1100 m and 1300 m in far eastern New Britain, although a further specimen in BPBM is labelled "New Britain Gazelle Pen. Talliligap, 300 m, 17–18.XII.1962"; "J. Sedlaceck Collector BISHOP" (Parsons, 1989a). The type series of *D. m. messalina* were collected by W.M. Brandt at Guava, Bougainville, at c. 1300 m and in Guadalcanal specimens of *D. m. orientalis* were collected at the summit of Mount Popomanaseu at 2327 m (Tennent, 1997).

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An Unusual Micromorphic Brachiopod from the Middle Cambrian of North-Eastern New South Wales, Australia

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ABSTRACT. *Anomalocalyx cawoodi* new genus and new species, from Middle Cambrian (Floran-Undillan) allochthonous limestone clasts of the Murrawong Creek Formation, north eastern New South Wales, is characterised by a deep, tapering, conical ventral valve with a pair of simple teeth, an arched pseudodeltidium, well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, and a presumed calcium carbonate shell composition, all suggesting an affinity with the Brachiopoda. *Anomalocalyx cawoodi* also possesses a number of unusual morphological features including an elongate, tapering interior tube extending along the inner posterior margin of the ventral valve, under the pseudodeltidium, that may be interpreted as a spondylium. Though possible cnidarian and molluscan affinities are fully explored, the weight of available evidence suggests the affinities of *A. cawoodi* are with the Brachiopoda.

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Williams *et al.* (1996) erected five new classes of brachiopods united by a number of shared synapomorphies within the subphylum Rhynchonelliformea including, (*a*) the presence of a pair of calcareous shells held together by an articulatory device at the posterior hinge line between the two shells, (*b*) an acoelomic pedicle core, and (*c*) the presence of a diductor system to control the opening of the shells. Williams *et al.* (1996) placed another calcareous class, the Craniata, characterised by a lack of articulation and functional pedicle, in a separate "inarticulate" subphylum. All five rhynchonelliform classes are represented in the Cambrian radiation and display a wide range of unusual morphological adaptations, particularly with regard to valve articulation, musculature and pedicle opening (Popov, 1992; Popov *et al.*, 1996; Williams *et al.*, 1996). Typical morphological variations manifest in these early groups include the development of simple, presumably primitive, articulation mechanisms as exemplified by early obolellids (such as *Bicia* Walcott), kutorginids and nisusiids (Roberts & Jell, 1990; Popov, 1992; Popov *et al.*, 1996), and the evolution of unique features in a number of short-lived taxa. Examples of such features include the unusual spoon-shaped apical plate and supporting pedestal in the ventral valve of the naukatid genera *Bynguanoia* Roberts

(in Roberts & Jell, 1990) and *Oina* Popov & Tikhonov, 1990, the arcuate plate along the hingeline in the ventral valve of the monospecific taxon *Bajarinovia* Aksarina & Pelman, 1978, and the posterior plate or colleplax in chileids (Popov *et al.*, 1996).

In addition to taxa that can, more or less, be comfortably placed within the concept of the phylum Brachiopoda (or Phylum Brachiozoa, subphylum Brachiopoda *sensu* Cavalier-Smith, 1998), there are a number of aberrant Cambrian organisms that secreted bivalved calcareous shells that cannot be placed in the Brachiopoda with any confidence. As an example, the Early Cambrian taxa *Apistoconcha* and *Arroonia* from the Flinders Ranges, South Australia (Conway Morris & Bengtson, in Bengtson *et al.*, 1990), and *Tianzhushanella* from China (Lui, 1979), are brachiopod-like in possessing a pair of calcareous shells with a posterior hinge axis of articulation, and a plane of bilateral symmetry bisecting the midline of both valves. However, the overall form of the valves, and the unique nature of the articulatory mechanism in these taxa, led Conway Morris & Bengtson (in Bengtson *et al.*, 1990: 184) to conclude that they were not true brachiopods, but possibly represented a sister lophophorate lineage. Parkhaev (1998) recently placed *Apistoconcha* and *Tianzhushanella* in a new Class, the Siphonoconcha, and suggested an affinity with the Mollusca or Stenothecoida, rather than with the Brachiopoda.

The focus of this paper is to describe the unique features of another aberrant calciate brachiopod taxon, from the Middle Cambrian Murrawong Creek Formation, northeastern New South Wales, Australia, and to probe the functional morphology and possible zoological affinities of this problematic organism.

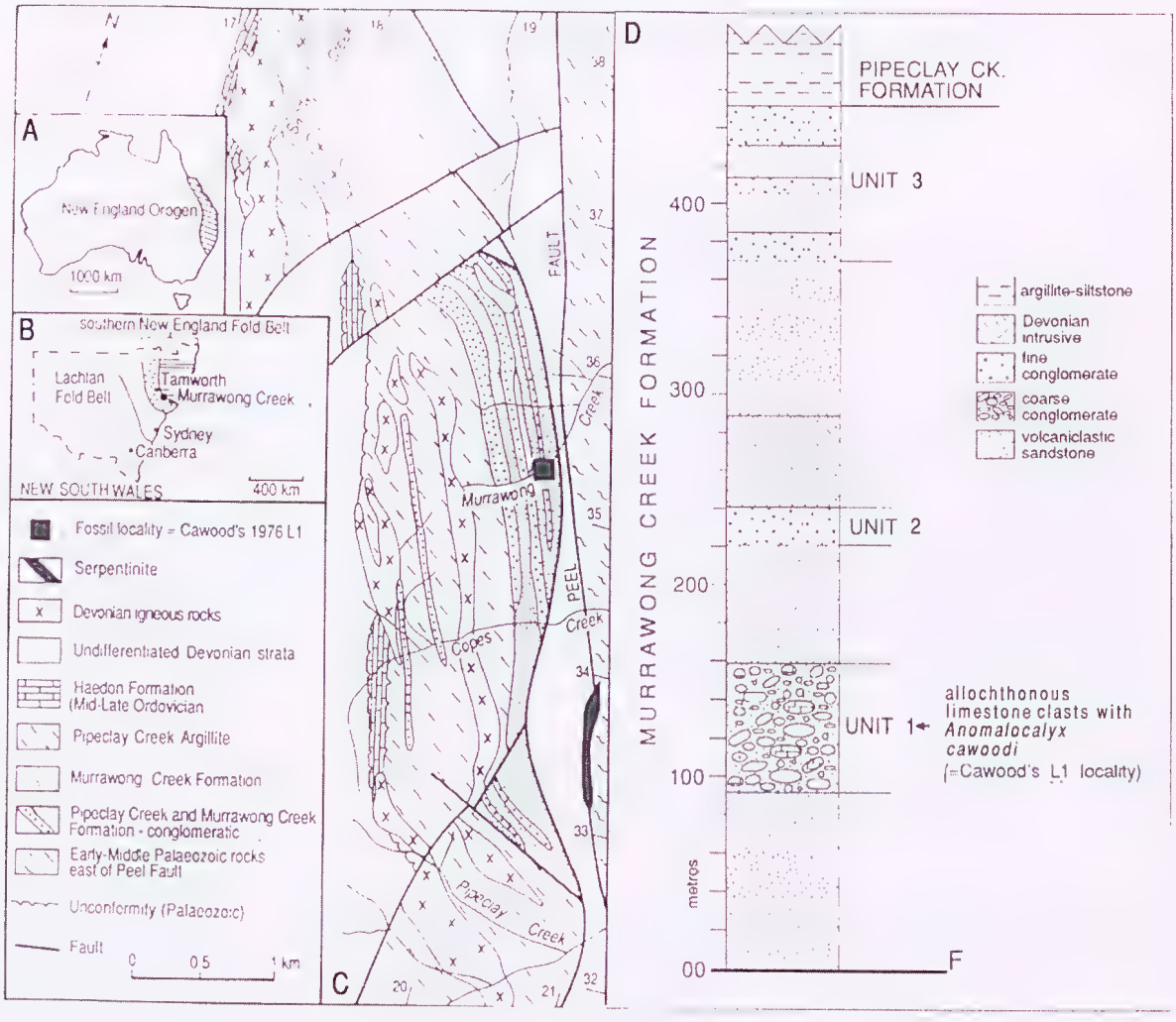

Figure 1. A, generalised map of Australia showing extent of rocks associated with the New England Fold Belt. B, generalised map showing exposures of the southern New England Fold Belt and the locality of the Murrawong Creek area. C, geological map of the Murrawong Creek–Copes Creek area (modified after Leitch & Cawood [1987]). Black box depicts area where 21 allochthonous limestone clasts were re-collected in 1992 from Cawood's (1976) original L1 locality, Unit 1 in Murrawong Creek (grid reference: $198_7\ 352_4$, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°96'08"E). D, type section of the Murrawong Creek Formation, along Murrawong Creek, showing sampled conglomerate horizon, Unit 1 of Leitch & Cawood, 1987 (= Cawood's [1976] L1 locality). Modified after Leitch & Cawood, 1987, fig. 2.

Geological setting and age

The geology, stratigraphy and depositional environment of the Murrawong Creek Formation have been outlined in some detail by Brock (1998a,b), so only a summary is presented here. The Murrawong Creek Formation (Cawood, 1980) is the oldest of three lithostratigraphic units in the Copes Creek-Murrawong Creek region of the southern New England Fold Belt, with sporadic outcrops in a 4.5 km north–south trending tract of interbedded siltstone, sandstone and conglomerate, some 25 km south-southeast of Tamworth, 31°18'08"S 151°06'28"E (Fig. 1A–C; Cawood, 1976, 1980; Leitch *et al.*, 1988; Leitch & Cawood, 1996). The type section, along Murrawong Creek, consists of 450 metres of poorly outcropping, interbedded coarse to fine debris flow conglomerates, turbiditic sandstone, siltstone, siliceous mudstone and ash-fall tuffs (Fig. 1D). The base of the section is faulted against undifferentiated ?Devonian metasediments. Leitch & Cawood (1987, fig. 2) recognised three conglomerate horizons in the Murrawong Creek Formation, informally designated Units 1–3. Unit 1, the coarsest of the three units (Fig. 1D), includes 85 m of poorly outcropping, polymictic paraconglomerate with angular to subrounded, mostly volcanic, clasts (0.01–1.5 m in diameter) set in a poorly sorted sand to granule grade volcaniclastic matrix. The largest clasts are represented by fossiliferous limestones (Fig. 2).

Provenance investigations of the cobble and pebble sized igneous clasts from the Murrawong Creek Formation revealed that the clasts are from a low-K orogenic suite, and the absence of detritus characteristic of continental crust is consistent with an interpretation favouring derivation from an intra-oceanic island arc rather than a continental margin arc (Leitch & Cawood, 1987, 1996). The presence of small quantities of volcanic beta quartz fragments in the allochthonous limestone clasts also implies proximity to an island arc (Engelbretsen, 1996). The allochthonous volcaniclastic debris of the Murrawong Creek Formation and the conformably overlying Pipeclay Creek Formation were probably deposited as gravity flows in an inner submarine environment into relatively deep water conditions (Leitch & Cawood, 1987: 635) from an eroded western source (Leitch & Cawood, 1987; Leitch *et al.*, 1988). The faunal content of the limestone clasts includes diverse trilobite assemblages (Sloan, 1991), lingulate brachiopods (Engelbretsen, 1996), calciate brachiopods (Brock, 1998a), molluscs (Brock, 1998b) and an array of undescribed small shelly fossils that indicate the original setting for the fossiliferous carbonates was a relatively shallow-water carbonate platform, possibly fringing a volcanic island or islands.

The trilobite assemblage from the allochthonous limestone clasts (see Brock [1998a,b] for details of taxa) containing the new brachiopod *Anomalocalyx cawoodi*

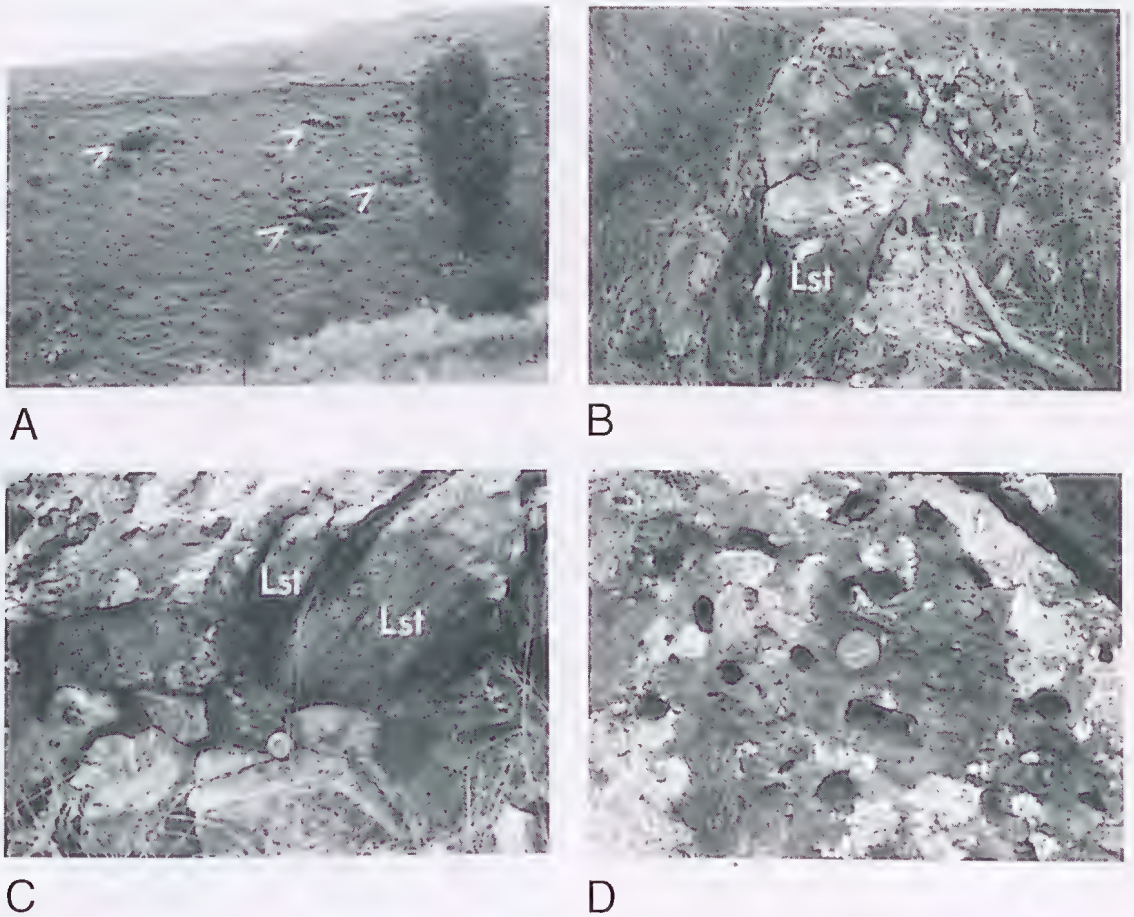

Figure 2. Field photographs of the Murrawong Creek Formation. A, wide angle shot, looking south, at some of the conglomeratic exposures of Unit 1 (arrowed); Murrawong Creek in foreground. B, lenticular, subrounded fossiliferous limestone clast (Lst), set in coarse volcaniclastic matrix of Unit 1. C, close-up of lenticular limestone clasts (Lst) in volcaniclastic matrix of Unit 1. D, weathered clast cavities in Unit 1 matrix. Lens cap 55 mm across in photographs B–D.

support an age spanning the *atavus–punctuosus* zones (Floran-Undillan Stages) using the Australian Middle Cambrian time-scale (Shergold, 1995).

Stewart (1995) reported the discovery of an assemblage of paraconodonts including *Muellerodus, Herzina, Prooneotodus* and *Furnishina*, and a number of minute forms similar to *Clavohamulus* and *Westergaardodina* from a dark, thinly bedded, spiculitic chert of the Pipeclay Creek Formation (Fig. 1D) in Copes Creek. The abundance of paraconodonts and the lack of euconodonts is consistent with a Middle Cambrian to early Late Cambrian age for this formation. It is thus clear that the Middle Cambrian allochthonous limestone clasts of the conformably underlying Murrawong Creek Formation are set in a matrix of similar age, as originally interpreted by Cawood (1976, 1980).

Preservation

All known specimens of *Anomalocalyx cawoodi* are preserved as epitaxial coatings of epidote. This type of preservation has previously been reported from the Murrawong Creek Formation in the coralomorph taxon *Tretocylichne perplexa* by Engelbretsen (1993: 55). A similar type of preservation, consisting of phosphatic epitaxial coatings, has also been described in the bivalve *Pojetaia runnegari* (Runnegar & Bentley, 1983) and the brachiopod-like taxon *Apistoconcha* (Bengtson *et al.*, 1990: 171, fig. 113).

The epidote coating covers all inner and outer surfaces of *Anomalocalyx*, faithfully replicating elements of the external and internal morphology, including fine surface detail. The internal space between the inner and outer layers of the coating attests to an original calcareous shell composition subsequently dissolved during acetic acid processing. The presence of a calcareous shell in *Anomalocalyx* is supported by the fact that only taxa known to possess a calcareous shell (e.g., articulate brachiopods, *Nisusia* and *Arctohedra*, molluscs, chancelloriids, and hyolithids) are preserved in a similar manner.

The preservation of *Anomalocalyx* ranges from fine to very coarse, resulting in a wide variation of gross morphology, especially in shell outline, the shape of the coniform ventral valve, and the preservation of fine features of the external ornament.

Systematic palaeontology

All type specimens are held in the Australian Museum (AM); registration numbers are given below.

Phylum **Brachiopoda** Dumeril

Subphylum **?Rhynchonelliformea** Williams, Carlson, Brunton, Holmer & Popov, 1996

Class, Order, Superfamily, Family **Uncertain**

Anomalocalyx n.gen.

Type species. *Anomalocalyx cawoodi* n.sp.

Diagnosis. Minute, deeply coniform, tapering ventral valve with very high, variably convex to flattened, catacline to weakly procline, interarea; delthyrium narrow, covered for entire length by a well-developed, evenly convex pseudodeltidium. Radial costae low, wide, anteriorly bifurcating, becoming fluted at commissural margin. Costae crossed at more or less regular intervals (70–100 μm) by low, undulose concentric growth lamellae. Valve outline variably subquadrate to subhexagonal. Teeth simple, rounded, dorsally directed, nub-like projections situated on the posterior valve wall either side of the delthyrium; an elongate, tapering, tube-like structure extends ventrally along the entire length of the delthyrial cavity directly under the convex pseudodeltidium. Dorsal valve with well-developed incurved umbo, broad median sulcus and anterior tongue. Interior with small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Notothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Discussion. *Anomalocalyx* displays a number of features indicative of a brachiopod assignment. These include, (*a*) a bivalved shell with the plane of bilateral symmetry bisecting the midline of both valves, (*b*) a pair of simple dorsally directed, nub-like teeth projecting from the posterior shell wall of the ventral valve, (*c*) a high, flattened ventral interarea bisected medianly by an elongate delthyrium covered by a prominent, arched pseudodeltidium, (*d*) well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, (*e*) a convex dorsal valve with simple socket plates, and (*f*) an inferred calcium carbonate shell composition. The presence of a calcareous shell composition, simple teeth in the ventral valve with an arched pseudodeltidium covering the delthyrium and dorsal sockets either side of a wide notothyrial gap conforms, at least partly, with the concept of the subphylum Rhynchonelliformea as outlined by Williams *et al.* (1996: 1192). *Anomalocalyx* is therefore referred, with some hesitation, to the Rhynchonelliformea.

The lack of information regarding muscle scars, mantle canal pattern and nature of the ventral umbo in *Anomalocalyx* precludes confident assignment to higher taxonomic levels within the Brachiopoda at the present time. The presence of a well-developed, convex pseudodeltidium flanked by flattened propareas in the ventral valve and a wide, triangular, open notothyrium (lacking a cardinal process) bordered by socket plates in the dorsal valve indicates *Anomalocalyx* may have some relationship to the order Kutorginida (Popov *et al.*, 1997). However, kutorginids are characterised by a large posterior median opening that is interpreted to have been the opening of a posteromedianly directed anus. The highly incurved dorsal valve and the nature of the articulation of the valves indicates no such opening existed in *Anomalocalyx* (Fig. 3C). Though some kutorginids, such as *Nisusia alaica* (Popov &

Tikhonov, 1990, pl. 3, fig. 23), possess moderately coniform ventral valves, none have the exaggerated form of *Anomalocalyx*, nor has any been described with an interior tube.

The elongate, irregular, tapering conical shape of the ventral valve of *Anomalocalyx* (Figs. 3C, 4A–L), though unusual amongst Cambrian calciate brachiopod orders, can be found in a few highly specialised, aberrant post-Cambrian taxa, such as the Silurian triplesiid *Onychotreta* Ulrich & Cooper (see Amsden, 1968), the highly specialised cemented ventral valves of the Permian richthofenioid brachiopods *Cyclacantharia* and *Sacchinella* (see Cooper & Grant, 1975), and the Permian nasute (coralliform) gemmellaroid genera *Cyndalia* and *Gemmellaroia* (Grant, 1993). *Cyndalia*, in particularly, displays a remarkable number of features similar to *Anomalocalyx*. Both taxa are micromorphic with calcium carbonate shells, and possess an elongate, tapering ventral valve (extravagant in *Cyndalia*) with well-developed pseudodeltidium. Though a short pedicle tube is present in species of the obolellid genus *Trematobolus* (Geyer & Mergl, 1995), the elongate tube-like structure situated directly under the arched pseudodeltidium and extending along the entire ventral wall of the ventral valve in *Anomalocalyx* has not previously been described in a Cambrian articulate brachiopod. Geyer & Mergl (1995) suggested the tube in *Trematobolus* probably housed a specialised pedicle similar to that found in *Discinisca*. The function of this tube in *Anomalocalyx* remains enigmatic, but it shows a remarkable similarity to the elongate, tapering tube-shaped structure in *Cyndalia* (see Grant, 1993, fig. 6) described as a tube-like spondylium produced by the coalescence of dental plates and a median septum, suggesting they formed a moving muscle attachment area (Grant, 1993: 55). The lateral margins of the tube-like structure in *Anomalocalyx* appear as though they are attached either side of the delthyrium, directly under the dorsally directed nub-like teeth (Figs. 3B, 4A,J–K,M), as would be expected if the structure were a spondylium for muscle attachment (Fig. 3C). If a spondylium interpretation is accepted, the function of the u-shaped groove on the outer surface of the spondylial tube (Figs. 3B, 4J) remains enigmatic. The fact that all ventral valves of *Anomalocalyx* have a broken apex makes it difficult to determine the presence or absence of an apical pedicle foramen. It seems unlikely that the tube actually housed a pedicle given the extraordinary length of the tube inside the ventral valve.

Close affinity between *Anomalocalyx* and *Cyndalia* is unlikely given their disjunct stratigraphic positions. The degree of morphological similarity between these two taxa may well be the result of convergent evolution, reflecting an analogous evolutionary response to specialised environmental circumstances. The ecology of both taxa is imperfectly known, but Grant (1993: 59) envisaged *Cyndalia* inhabiting a turbid, muddy, shallow water, lagoonal setting. Given the allochthonous setting of the *Anomalocalyx*-bearing clasts, the original environmental setting is even more difficult to reconstruct, but contemporaneous faunal assemblages suggest *Anomalocalyx*

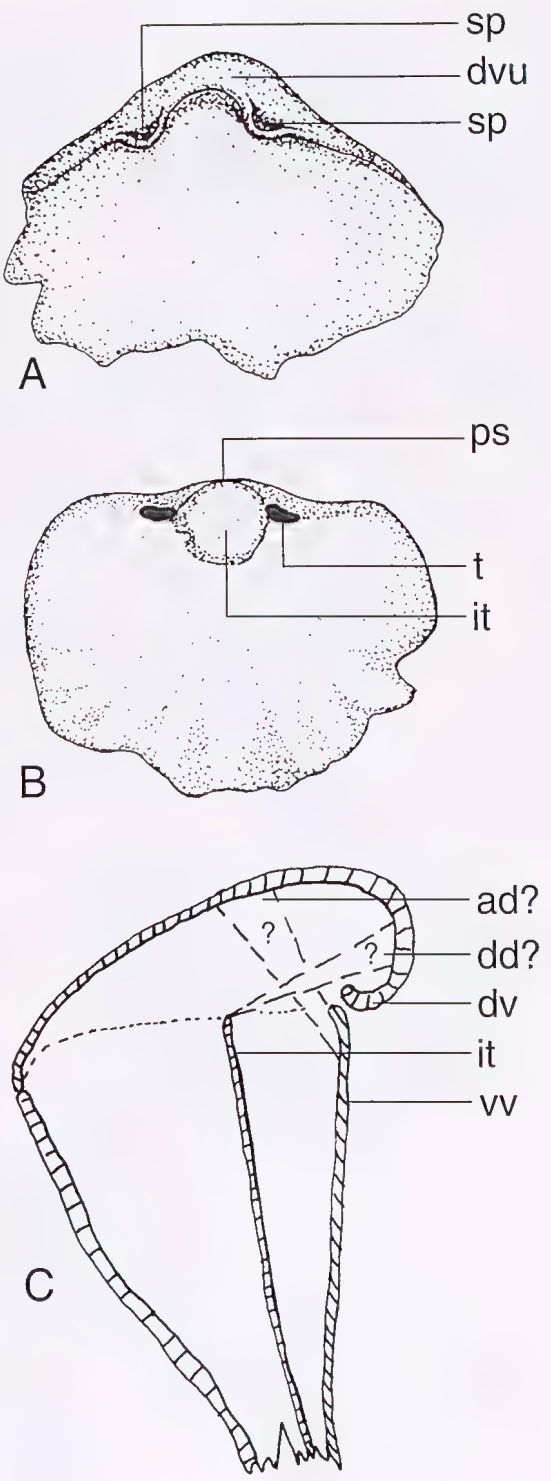

Figure 3. A, dorsal valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on AM F107869; valve width 1 mm. B, ventral valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on numerous specimens; valve width approximately 1.5 mm. C, tentative reconstruction along axial longitudinal plane of conjoined specimen of *Anomalocalyx cawoodi* n.gen. et n.sp. showing speculative position of adductor and diductor muscles. The interior tube in the ventral valve is reconstructed as a spondylial platform. Abbreviations: ad?, speculative adductor muscle; dd?, speculative diductor muscle; dv and dvu, dorsal valve and dorsal valve umbo; it, interior (spondylial) tube; ps, pseudodeltidium; sp, socket plates; t, tooth; vv, ventral valve.

was probably associated with a shallow water carbonate platform fringing a volcanic island arc (Brock, 1998a,b). The elongate ventral valves of both taxa are similar to those found in some rudist bivalves, and are best explained as an adaptation for keeping the aperture elevated above the muddy substrate (Grant, 1993: 59). However, because of the millimetric dimensions of the shell, an infaunal, epifaunally attached, or cryptic life habit cannot be completely ruled out.

The possibility that *Anomalocalyx* may represent a new type of coral-like organism similar to *Tretocylichne* Engelbretsen, 1993 or the operculate *Cothonion* Jell & Jell, 1976 cannot be completely ruled out. However, close comparison of these two unusual forms reveals that *Anomalocalyx* lacks the octagonal outline, longitudinal septa on the inner surface of the calyx, perforate expanded base, and thecal budding characteristic of *Tretocylichne* Engelbretsen, 1993. The slightly older operculate genus, *Cothonion* described by Jell & Jell (1976) from the early Middle Cambrian Coonigan Formation, western New South Wales has a similar shape to the putative ventral valve of *Anomalocalyx*, but *Cothonion* can be discriminated by the presence of strong internal septa, and the operculum is generally flattened or upturned (concave) at the midpoint, and internally, is characterised by the development of strong radial septa. No coralomorph taxon yet described has been discovered with the brachiopod-like teeth or the interior tube characteristic of *Anomalocalyx*.

Etymology. The Greek word *anomalos* for unusual, abnormal, deviating from the general rule is combined with *kalyx* (Greek) for cup.

Anomalocalyx cawoodi n.sp.

Figs. 3A–C, 4A–P

Type material. HOLOTYPE: ventral valve from clast W10, AM F97383, Fig. 4A–E. PARATYPES 11 ventral valves (VV hereafter) and 22 dorsal valves (DV hereafter) as follows: 3 VV, AM F97384 (Fig. 4F–I), AM F107867 (Fig. 4J–L) and AM F97385 (Fig. 4M); 3 DV, AM F107868 (Fig. 4N), AM F107869 (Fig. 4O) and AM F107870 (Fig. 4P); 6 DV, AM F112571–76, and 2 VV, AM F112577–78, from clast W1; 3 DV, AM F112579–81, from clast W3; 2 DV, AM F112582–83, and 2 VV, AM F112584–85, from clast W10; 2 DV, AM F112586–87, and 1 VV, AM F112588, from clast W38; 6 DV, AM F112589–94, and 3 VV, AM F112595–97, from clast W/L1/S4.

Type locality. Allochthonous limestone clasts, Unit 1, Murrawong Creek Formation. Equivalent to Cawood's (1976) original L1 locality (Fig. 1C). Grid Reference: 198_7 352_4, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°06'28"E.

Diagnosis. As for genus.

Description. Shell minute (maximum width 2 mm, maximum length 1.8 mm), with variable shell outline ranging from semicircular to subquadrate to subhexagonal. Maximum shell width approximately mid-valve. External ornament consists of between 10–14 low, wide (0.2–0.3 mm), rounded costae increasing anteriorly by bifurcation, becoming fluted at the commissure. Intercostal furrows wide and shallow. Costellation and intercostal regions crossed by a series of continuous, low and undulose concentric growth lamellae spaced at intervals of approximately 0.1 mm.

Ventral valve deep, curved, irregularly conical, tapering apically, with high (max. 3.0 mm), variably developed, catacline to weakly procline interarea. Interareas flattened to weakly convex; barely perceptible in some specimens as they merge and arch medianly forming a single convex pseudodeltidium. Concentric lamellae cross interareas and pseudodeltidium. All known ventral valves broken, so apical morphology (including presence or absence of a foramen) unknown. Interior of ventral valve with an elongate, tapering tube-like structure (maximum width 0.6 mm) extending ventrally along the entire delthyrial cavity directly under the pseudodeltidium. A u-shaped groove (0.15 mm wide), narrowing gradually with the ventral direction of valve taper, present on anterolateral surface of tube. Short, stubby, dorsoventrally flattened, convergent teeth arise as simple, dorsoanteriorly directed projections from posterior shell wall in most specimens. Muscle scars not preserved.

Putative dorsal valve strongly convex, with short, curved hingeline and broad, shallow, anteriorly widening, median sulcus. Umbo enlarged and recurved, almost forming a hood over the notothyrium. External ornament similar to ventral valve, though radial costae tend to arise via implantation rather than bifurcation. Small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Nothothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Remarks. Though no articulated specimens of *A. cawoodi* have been recovered, a number of convex valves of appropriate size, with similar outline and ornament to the ventral valve have been identified as matching dorsal valves (Figs. 3A, 4N–P). Internally, the cardinal area of the putative dorsal valve is very simple, with a wide notothyrium bordered by simple socket-like plates excavated into the posterior shell wall (Figs. 3A, 4N–O). Multiple epitaxial coatings of these valves is sometimes so thick that the socket plates become extravagantly enlarged, making the edges of the socket-plates project forward like teeth, mimicking the morphology of a simple ventral valve. Inspection of paratypic dorsal valves without multiple coatings of epidote display an unmistakable, but simple, dorsal valve morphology (Figs. 3A, 4N–O). The articulatory mechanism in *A. cawoodi* was clearly very rudimentary. The simple, rounded, nub-like teeth must have slotted into the matching sockets excavated in the posterior shell wall of the dorsal valve. There is no evidence of a cardinal process. The dorsal valve has an unusually enlarged, incurved umbo, almost forming a notothyrial hood, and this may have been the site for direct muscle attachment (Fig. 3C). A consequence of the enlarged dorsal umbo is that, when articulated, a restricted valve gape must have resulted, and there would

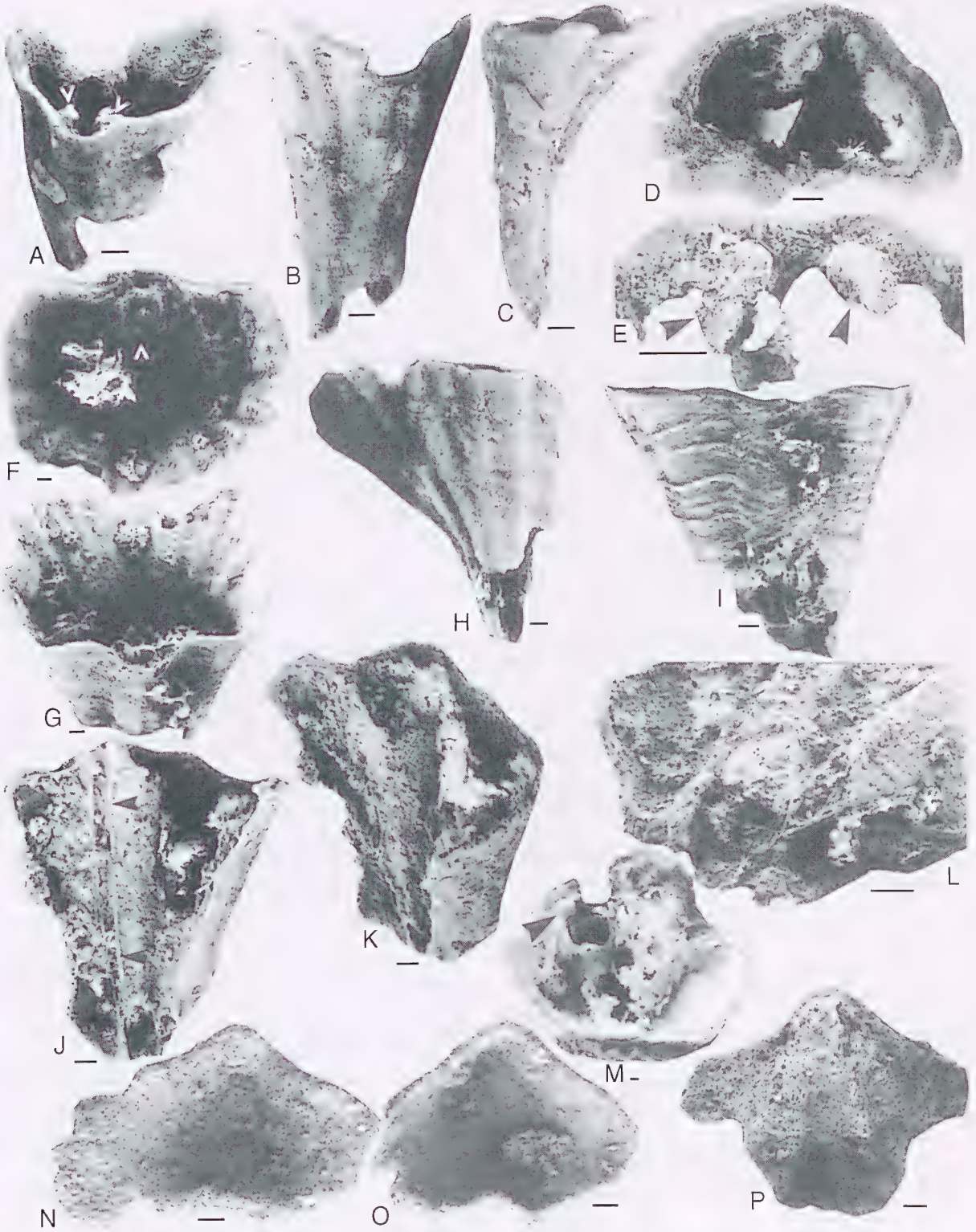

Figure 4. A–P, *Anomalocalyx cawoodi* n.gen. et n.sp. A–E, AM F97383, holotype from clast W10: A, oblique posterior view of holotype ventral valve showing teeth (arrowed); B, anterior view showing sulcate commissure; C, lateral view showing elongate, curved and tapering ventral valve; D, interior view; E, close-up of teeth (arrowed) in holotype. F–I, AM F97384, paratype ventral valve from clast W10: F, oblique interior showing interior tube (arrowed) with teeth broken away in specimen; G, oblique posterior view showing well-developed interarea and arched pseudodeltidium; H, lateral view; I posterior view showing undulose concentric growth lines. J–L, AM F107867, broken paratype ventral valve from clast W1: J, broken interior of ventral valve showing tapering interior (spondylial) tube with u-shaped external groove (arrowed); K, oblique view showing interior tube; L, close up of posterior portion of interior tube (infilled with sediment). M, AM F97385, paratype ventral valve from clast W10, showing dorsal portion of interior tube and a nub-like tooth (arrowed). N, AM F107868, interior of abraded paratype dorsal valve from clast W1 showing wide notothyrial gap. O, AM F107869, interior of abraded paratype dorsal valve from clast W1 showing simple socket plates (arrowed). P, AM F107870, exterior of abraded paratype dorsal valve from clast W1 showing anterior tongue. All scale bars 100 μm.

have been no posterior gap between the posterior edge of the pseudodeltidium and the dorsal umbo for a pedicle opening.

Etymology. In honour of Dr Peter Cawood, who discriminated and named the Murrawong Creek Formation and was the first to discover Cambrian fossils in this formation.

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Systematics, Biostratigraphy and Evolution of the Late Ludlow and Přídolí (Late Silurian) Graptolites of the Yass District, New South Wales, Australia

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ABSTRACT. Graptolites from the Yass district of New South Wales include important material from: low in the Black Bog Shale; from the Yarwood Siltstone Member; 2 levels high in the Black Bog Shale; 2 levels low in the Rosebank Shale; low in the Cowridge Siltstone; and in the lower part of the Elmside Formation. The faunas from the lower 4 levels are late Ludlow (early Late Silurian), and the higher 4 levels are Přídolí (late Late Silurian).

Twenty-seven graptolite taxa, a considerable increase on previous records from Yass, have been identified in the late Ludlow and Přídolí of the district. These taxa enable the Ludlow-Přídolí boundary to be identified some 20 m above the base of the Rosebank Shale (Booroo Ponds Group); our stratigraphically highest collection from the Elmside Formation is latest Přídolí, supporting the previous placement of the base of the Devonian approximately midway through the Elmside Formation (Barambogie Group). The following graptolite Biozones have been identified: *praecornutus, cornutus, parultimus, bouceki* and *transgrediens*. Twenty Yass taxa are described, including the new species *Bohemograptus paracornutus, Pristiograptus shearsbyi, Neocucullograptus? yassensis* and *N.? mitchelli* and the new subspecies *Monograptus perneri elmsidensis* and *M. formosus jenkinsi*. The following are recorded from Australia for the first time: *Bohemograptus praecornutus* Urbanek, 1970; *Crinitograptus operculatus* Münch, 1938; and *Pristiograptus kolednikensis* Přibyl, 1940. *Dictyonema* sp. cf. *D. sherrardae* Rickards *et al.*, 1995 and *D. elegans* Bulman, 1928 are considered late evolutionary derivatives of long-ranging dendroid species. *Linograptus posthumus introversus* Rickards & Wright, 1997 is interpreted as a short-lived, late Ludlow offshoot of the long-ranging *L. p. posthumus* Richter, 1875. *Bohemograptus praecornutus* is regarded as the ancestor of *B. paracornutus*, the *B. cornutus* evolutionary plexus being recognised for the first time in Australia. Late forms of *Pristiograptus dubius* (Suess, 1851) probably gave rise to *P. shearsbyi* n.sp. and *Pristiograptus kolednikensis* probably arose in the basal Přídolí from the late Ludlow *P. fragmentalis* (Bouček, 1936). Some material described and discussed by Brown & Sherrard (1952) is reinterpreted.

Bohemograptus paratenuis n.sp. is proposed for material assigned by Urbanek (1970) to *B. bohemicus* aff. *tenuis* (Bouček, 1936); this species is known only from Poland.

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The Yass Silurian sequence of New South Wales has been recognised as one of the most important developments of the system in Australia (Jell & Talent, 1989). Among the fossil groups abundantly represented in the Yass strata, conodonts and graptolites are the most important for determining the age relationships of the strata; the conodont faunas were described by Link & Druce (1972) but the graptolites have been, by comparison, poorly known. In this paper we identify the graptolite faunas from a number of stratigraphic levels in the Yass sequence, and determine the ages and evolutionary relationships of the faunas.

The early explorer-geologist Strzelecki (1845) was the first to note the occurrence in the Yass district of strata we now recognise as Silurian. Graptolites from the Yass Silurian were first noted by the local schoolteacher, John Mitchell (1886, 1888: from "Bowning Beds, Bowning" and "Bell [sic] Vale"). The first brief graptolite description (as "allied to *M. dubius*") and illustration were by T.S. Hall (1903: Bowning Series, Belle Vale). Although "Belle Vale" is still a well-known property on the Black Range Road in the Yass district (Fig. 1), these reports are of historic interest only as the locality and material are not recognisable from published data. A.J. Shearsby, a local photographer and keen amateur geologist, noted in 1912 the graptolites *Monograptus* (?) and *Dendrograptus* from strata identified by him as the "Barrandella shales".

The stratigraphic terminology for the Silurian strata of the area has evolved considerably from the pioneering descriptions by Shearsby (1912) and Brown (1941), to the current stratigraphic terminology proposed by Link (1970), followed by Link & Druce (1972) in their seminal studies of conodonts from the Yass Silurian, and finally modified by Cramsie *et al.* (1978).

Sherrard & Keble (1937) described Ordovician and Silurian graptolites from the Yass area. Surprisingly (in view of the abundant graptolites at other levels in the Yass Silurian sequence) the Silurian graptolites they described were Přídolí forms from near "Silverdale" NNW of Yass (Fig. 1), under the names of *Monograptus flemingii* (Salter), *M.*

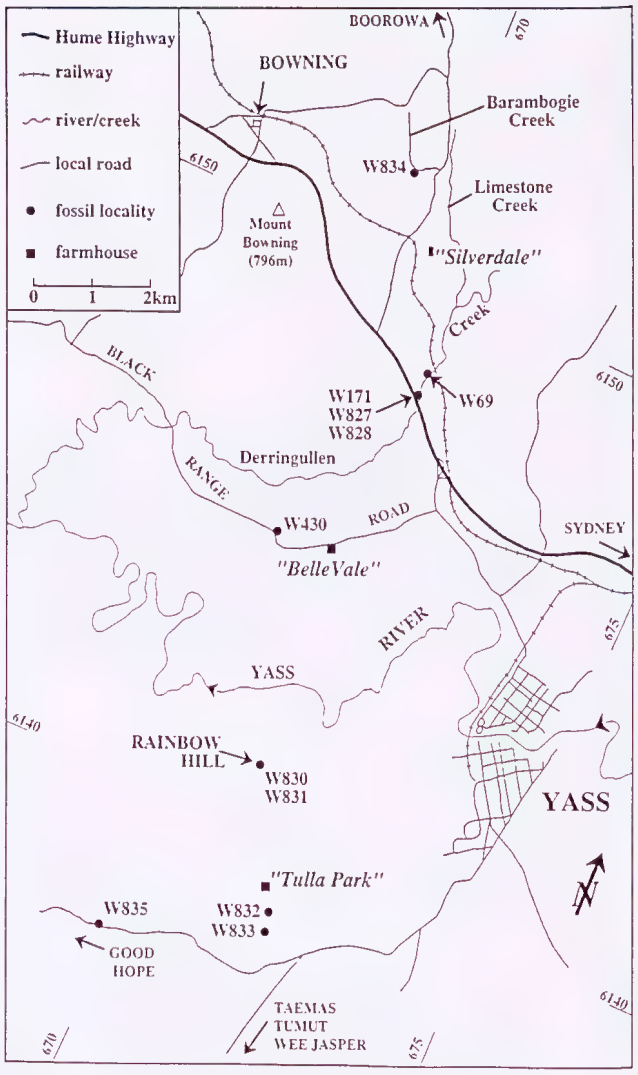

Figure 1. Locality map for the Yass district. Geological details can be obtained from Link & Druce (1972). The 3 and 4 digit numbers adjacent to short lines along the figure margins indicate the metric grid for the Yass 8628-S 50 000 map sheet.

Table 1. A comparison of previously identified graptolites from the Yass district, and present identifications of Yass graptolites.

Sherrard & Keble, 1937	Brown & Sherrard, 1952	Jaeger, 1967	Packham, 1968	this paper
	M. bohemicus	*M. bohemicus* subsp. B		*Bohemograptus paracornutus* n.sp.
M. cf. *nilssoni*	*M. nilssoni*	*Linograptus p. posthumus*		*L. p. posthumus*
				L. p. introversus
	M. roemeri	*M. bohemicus*		*B. paracornutus* n.sp.
	M. crinitus	*M. scanicus* group		*?L. p. posthumus*
M. cf. *tumescens*		*M. dubius* group	*M.* cf. *ultimus*	*M. parultimus*
M. flemingii	*M. salweyi*	*M. bouceki*		*M. bouceki*
M. cf. *vomerinus*		*M. transgrediens*		*M. transgrediens*
M. cf. *nilssoni*				
		M. bohemicus subsp. A		*B. praecornutus*
		M. formosus	*M. formosus*	*M. formosus*

cf. *tumescens* Wood, *M.* cf. *vomerinus* (Nicholson), *M.* sp. cf. *M. nilssoni* (Barrande) and *Dictyonema* sp.

A more significant step in the study of the graptolites of the Yass district was made by Brown & Sherrard (1952), who first drew attention to the existence of what has traditionally been known as the "*Monograptus bohemicus*" fauna at Yass. Subsequent work on this "*bohemicus*" fauna (now best known from Rainbow Hill) has been limited to a few preliminary comments by Jaeger (1967), which are discussed as appropriate in the taxonomic section of this paper. Brown & Sherrard described this "*bohemicus*" fauna under the names of *Monograptus bohemicus* Barrande, 1850, *M. nilssoni, M. crinitus* Wood, *M. roemeri* (Barrande) and *Dictyonema* sp. We have restudied their illustrated "*bohemicus*" material and conclude that it is (1) not *B. b. bohemicus* but *B. b. tenuis* (Bouček, 1936), and (2) possibly is not from Rainbow Hill but from exposures of a slightly different level (B, probably just below our level 2: see Fig. 2) high in the Black Bog Shale, possibly along strike towards the Yass River (Fig. 1). Some of Brown & Sherrard's illustrated graptolites are re-illustrated in Fig. 11 and re-identified in Table 1 herein. Brown & Sherrard also restudied the "Silverdale" fauna, from which they determined and described *Monograptus salweyi* (Hopkinson), *M.* sp. cf. *M. tumescens* Wood and *Dictyonema*.

Both Jaeger (1967) and Packham (1968) studied graptolites from levels other than those studied by Brown & Sherrard (1952). Packham identified *Monograptus formosus* Bouček, 1931b and *Monograptus* cf. *M. ultimus* Perner, 1899 from the Rosebank Shale at the junction of the (then) Hume Highway and Derringullen Creek, above the unit now known as the Rainbow Hill Marl Member of the Rosebank Shale (Link & Druce, 1972), and considered this fauna basal Přídolí, with which we concur.

Jaeger (1967) commented briefly on graptolites from three levels in the Yass sequence. Firstly, he studied the graptolite fauna previously studied by Sherrard & Keble (1937) from the lower part of the Cowridge Siltstone at the locality known as "Silverdale" (Fig. 1), which is close to our locality W834. He showed that these former workers had incorrectly identified *Monograptus bouceki* Přibyl, 1940 as *Monograptus salweyi* from this locality; he also recorded *Monograptus transgrediens* Perner, 1899 from his "Silverdale" material, and considered the fauna to be Přídolí. Secondly, he identified *Monograptus formosus* and "*M.* sp. of the *M. dubius* group" from Packham's (1968) locality, and the latter also from the locality near the Good Hope road (see Brown & Sherrard, 1952, fig. 1). Thirdly, he made interesting preliminary comments on the bohemograptids from below the Rainbow Hill Marl, from an unspecified locality. With regard to his collections from Yass (and Quarry Creek, cited by Jaeger, 1991), recent information suggests that these collections may be in the Humboldt Museum in Berlin.

The most recent advance in the study of Yass Silurian graptolites was by Jenkins (1982) who described a latest Přídolí fauna from the lower part of the Elmside Formation. Some Elmside material illustrated by Jenkins (1982) is refigured here in Fig. 12.

Despite the above record of graptolite research, the Yass sequence of Silurian graptolites has remained poorly known by world standards; in particular, the supposed "*Monograptus bohemicus*" fauna from the topmost beds of the Black Bog Shale has remained essentially unstudied for almost 45 years.

Our stratigraphically lowest specimens are from the Black Bog Shale, although Shearsby (1912), Jaeger (1967) and Cramsie *et al.* (1978) reported material from lower in the sequence. We have made new graptolite collections from most of the important localities mentioned by the above workers, as well as other localities, and now have 27 graptolite taxa from the area, spanning the Ludlow-Přídolí interval. This work has significantly extended the faunal diversity previously noted from most localities; some newly recorded taxa are surprisingly common in our collections.

Materials and method

Material cited and figured in this study is deposited in the Australian Museum; a supplementary collection is held for comparative purposes in the Sedgwick Museum, Department of Earth Sciences, University of Cambridge. "AMF" are Australian Museum numbers and "SM X." are Sedgwick Museum. Material reported by Jaeger (1967) has not been available for study, but it may be in the Humboldt Museum für Naturkunde, Berlin. However, with the exception of *Monograptus formosus* we have ample duplicate collections. Most taxa plotted on Fig. 2 are here both illustrated and described, but a few are merely illustrated. Elmside Formation specimens described by Jenkins (1982) have not been redescribed here, except for *M. formosus jenkinsi* n.subsp. (=*M. formosus* of Jenkins), *M. transgrediens* and *M. hornyi* (=*M.* cf. *angustidens* of Jenkins).

The graptolites are preserved in a variety of rock types from fine mudrock and shale to medium sandstones. Often they are in full relief. There is some slight tectonic deformation at some localities, and is indicated as appropriate on the illustrations; not all specimens from any one locality appear to be affected in the same way. There is some soft sediment deformation, especially of more slender species. However, in general the material is excellently preserved and more or less undeformed. The taxonomy is that recently used by Rickards *et al.* (1995), Rickards & Wright (1997) and Koren′ & Sujarkova (1997). Measurements of thecal spacing are given in the manner devised by Packham (1962), which we prefer to Howe's (1983) 2TRD technique: the latter we find less readable and more difficult to compare quickly with older methods of measurement. Σ is the distance from the sicular aperture to the most distal extremity of the first theca.

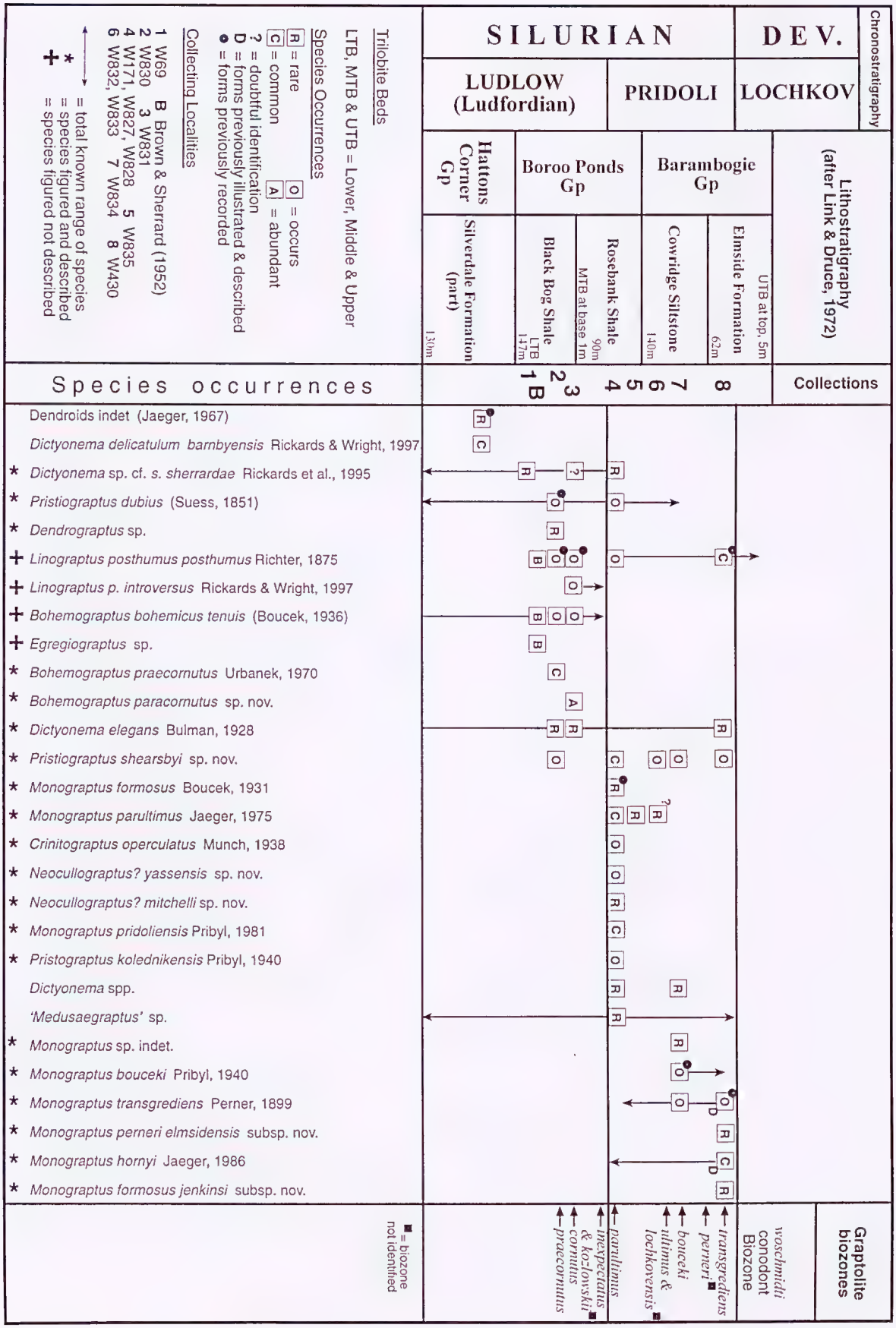
Chronostratigraphy
SILURIAN
DEV.
LUDLOW (Ludfordian)
PRIDOLI
LOCHKOV
Lithostratigraphy (after Link & Druce, 1972)
Hattons Corner Gp
Boroo Ponds Gp
Barambogie Gp
Silverdale Formation (part) 130m
Black Bog Shale LTB 147m
Rosebank Shale 90m MTB at base 1m
Cowridge Siltstone 140m
Elmside Formation 62m
UTB at top, 5m
Collections
1B 2 3 4 5 6 7 8
Species occurrences
Dendroids indet (Jaeger, 1967)
Dictyonema delicatulum barnbyensis Rickards & Wright, 1997
* Dictyonema sp. cf. s. sherrardae Rickards et al., 1995
* Pristiograptus dubius (Suess, 1851)
* Dendrograptus sp.
+ Linograptus posthumus posthumus Richter, 1875
+ Linograptus p. introversus Rickards & Wright, 1997
+ Bohemograptus bohemicus tenuis (Boucek, 1936)
+ Egregiograptus sp.
* Bohemograptus praecornutus Urbanek, 1970
* Bohemograptus paracornutus sp. nov.
* Dictyonema elegans Bulman, 1928
* Pristiograptus shearsbyi sp. nov.
* Monograptus formosus Boucek, 1931
* Monograptus parultimus Jaeger, 1975
* Crinitograptus operculatus Munch, 1938
* Neocullograptus? yassensis sp. nov.
* Neocullograptus? mitchelli sp. nov.
* Monograptus pridoliensis Pribyl, 1981
* Pristograptus kolednikensis Pribyl, 1940
Dictyonema spp.
'Medusaegraptus' sp.
* Monograptus sp. indet.
* Monograptus bouceki Pribyl, 1940
* Monograptus transgrediens Perner, 1899
* Monograptus perneri elmsidensis subsp. nov.
* Monograptus hornyi Jaeger, 1986
* Monograptus formosus jenkinsi subsp. nov.
Trilobite Beds
LTB, MTB & UTB = Lower, Middle & Upper
Species Occurrences
R = rare
C = common
O = occurs
A = abundant
? = doubtful identification
D = forms previously illustrated & described
• = forms previously recorded
Collecting Localities
1 W69 B Brown & Sherrard (1952)
2 W830 3 W831
4 W171, W827, W828 5 W835
6 W832, W833 7 W834 8 W430
* = total known range of species
+ = species figured and described
= species figured not described
Graptolite biozones
woschmidti conodont Biozone
parultimus
inexpectatus & kozlowskii
cornutus
praecornutus
bouceki
nilitmus & lochkovensis
transgrediens
perneri
■ = biozone not identified

Figure 2. Ranges of identified graptolites plotted against lithostratigraphy and proposed biostratigraphy and chronostratigraphy. Elmside Formation occurrences are partly after Jenkins (1982). The symbols indicating numbers of specimens are approximately: R, 1–10; O, 15–50; C, 50 to several hundreds; and A, thousands. The symbol B indicates the level of Brown & Sherrard's collections; only single slabs are in their collections, so abundances are unknown.

Systematic palaeontology

Class **Graptolithina** Bronn, 1849

Order **Dendroidea** Nicholson, 1872

Family **Dendrograptidae** Roemer, in Frech, 1897

Dendrograptus J. Hall, 1858

Type species. *Graptolithus hallianus* Prout, 1851; subsequently designated by J. Hall (1862).

Dendrograptus sp.

Fig. 3A

Material. A single specimen AMF 92368, from locality W830, *praecornutus* Biozone, late Ludlow, Black Bog Shale.

Description. The single fragment is a little over 7 mm long, with five branching divisions of typical *Dendrograptus* style. Autothecae are seen in one part and have a spacing of 20 in 10 mm. Dorsoventral stipe width is about 0.40 mm, assuming the lowest stipe is in true profile. Lateral stipe width is 0.15–0.40 mm, declining distally, suggesting that this portion of stipe is towards the extremity of the rhabdosome.

Remarks. *Dendrograptus* is a rare genus in the Silurian of NSW and only one specimen has been found in the Yass district. Rickards & Wright (1997) recorded five unidentifiable fragments from the Barnby Hills Shale; from the Quarry Creek region Rickards *et al.* (1995) recorded sparse, specifically unidentifiable fragments in the Wenlock and others, possibly conspecific with the Wenlock form, at two levels in the early Ludlow. It was suggested in the latter paper that the fragmentary nature of the rhabdosome, which is no less robust than other well-preserved dendroids occurring with them, may indicate a longer and more turbulent preservational history or, perhaps, a more distant, further inshore, provenance.

Dictyonema J. Hall, 1851

Type species. *Gorgonia retiformis* J. Hall, 1843; subsequently designated by Miller (1889).

Dictyonema sp. cf. *D. sherrardae sherrardae* Rickards *et al.*, 1995

Fig. 3B

?1952 *Dictyonema* sp.; Brown & Sherrard, p. 133, pl. VIII, fig. e.

cf. 1995 *Dictyonema sherrardae sherrardae* Rickards *et al.*, p. 20, figs. 11A–C, 12D,E, 13A,B.

Material. A small number of fragmentary specimens including: AMF 92369 from locality W69, Black Bog Shale from Ludlow, pre-*praecornutus* Biozone; and AMF 103037–44 from locality W171, Rosebank Shale, Přídolí, *parultimus* Biozone, ?AMF 44611 (Brown & Sherrard, 1952, pl. VIII, fig. e).

Description. Thecae with pronounced dorsal apertural process occupying fully half of the dorsoventral width of 0.80–0.95 mm and directed ventrally. Autothecal spacing about 20 in 10 mm. Bithecae not detected. Lateral stipe width about 0.30–0.40 mm.

Remarks. This is the first possible record of the *sherrardae* group in the Přídolí, as the two previously known Ludlow occurrences are in the *nilssoni* Biozone (Rickards *et al.*, 1995) and the *inexspectatus-kozlowskii* Biozone (Rickards & Wright, 1997). The Yass material is close to the type subspecies in thecal spacing and dorsoventral stipe width, but we have no data on dissepimental spacing and stipe spacing, and no information on dissepiment type. *Dictyonema s. mumbilensis* Rickards & Wright (1997: 215–216) from the late Ludlow *inexspectatus/kozlowskii* level of the Wellington district (and here reported from Barrandella Shale Member of the Silverdale Formation [Fig. 2] at Yass) is a more slender form with a higher thecal spacing which may represent an offshoot of the main lineage.

Dictyonema elegans Bulman, 1928

Figs. 3C,D

1928 *Dictyonema elegans* sp. Bulman, p. 52, text-fig. 26; pl. 6, figs. 2–3.

1984 *Dictyonema (Dictyonema) elegans* Bulman; Kraft, p. 402; pl. 1, figs. 2–4.

1995 *Dictyonema elegans* Bulman, 1928; Rickards *et al.*, p. 22, figs. 14C,D.

1997 *Dictyonema elegans* Bulman, 1928; Rickards & Wright, p. 214, figs. 5C, 8D.

?1997 *Dictyonema* cf. *elegans* Bulman, 1928; Rickards & Wright, p. 214, fig. 5D.

1997 *Dictyonema ?elegans* Bulman, 1928; Rickards & Wright, p. 214, fig. 6B.

Material. Upper beds of Black Bog Shale, late Ludlow: AMF 92366 from locality W830, *praecornutus* Biozone; AMF 102899 from W831, *cornutus* Biozone. One specimen (AMF 102890) from locality W430, late Přídolí; Elmside Formation, Black Range Road.

Description. Lateral stipe widths up to 0.25–0.30 mm and dorsoventral stipe widths 0.44–0.55 mm, including pronounced ventral processes. No obvious dorsal apertural processes. Interstipe spaces up to 0.40–0.60 mm. Stipe spacing approximately 20 in 10 mm, but the fragments do not allow a good measurement of dissepimental spacing. It is possible that the ventral apertural processes become spinose distally (see Fig. 3C) but these may, in fact, be slender dissepiments. Autothecal spacing about 30 in 10 mm.

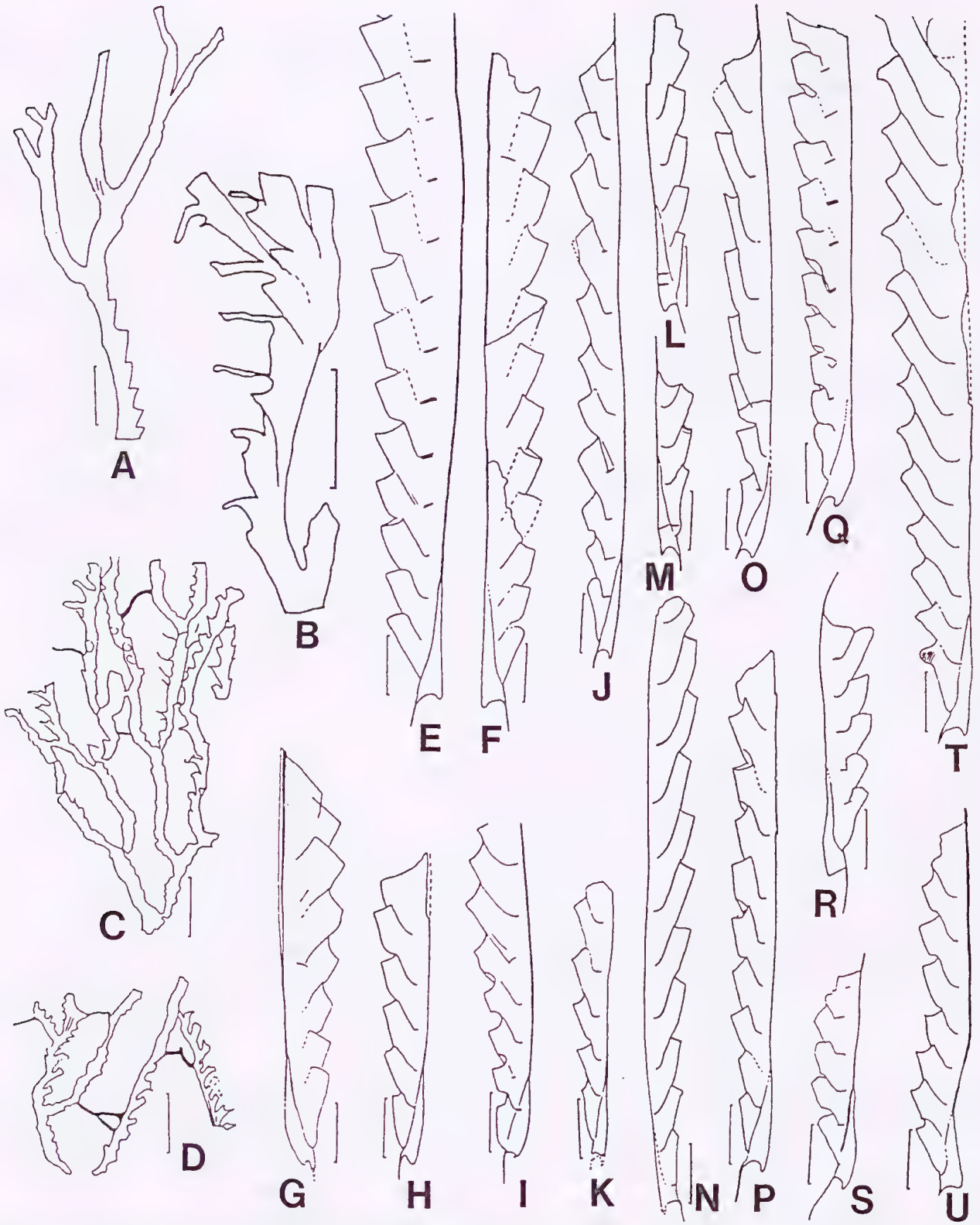

Figure 3. **A**, *Dendrograptus* sp., AMF 92368, W830, Black Bog Shale, *praecornutus* Biozone. **B**, *Dictyonema* sp. cf. *D. sherrardae sherrardae* Rickards *et al*., 1995, AMF 92369, W69, Black Bog Shale, Derringullen Creek. **C,D**, *Dictyonema elegans* Bulman, 1928; respectively AMF 102890, W430, Elmside Formation, *transgrediens* Biozone; and AMF 92366, W830, Black Bog Shale, *praecornutus* Biozone. **E,F**, *Pristiograptus kolednikensis* Přibyl, 1940, respectively AMF 92353–54, probably W171, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek. **G–I**, *Pristiograptus dubius* Suess, 1851, respectively AMF 92359, AMF 92356, AMF 92360, W830, Black Bog Shale, *praecornutus* Biozone. **J–P**, *Pristiograptus shearsbyi* n.sp., respectively AMF 92358, W830, Black Bog Shale, *praecornutus* Biozone; AMF 92385, W833, base of Cowridge Siltstone; AMF 92345, W827, Rosebank Shale, *parultimus* Biozone; AMF 92395, holotype AMF 92392 and AMF 92394, W834, Cowridge Siltstone, *bouceki* Biozone; AMF 92344, W827, Rosebank Shale, *parultimus* Biozone. **Q–S,U**, *Monograptus parultimus* Jaeger, 1975; respectively AMF 102894, W171, Rosebank Shale, *parultimus* Biozone; AMF 92361, W171, Rosebank Shale, *parultimus* Biozone; AMF 92383, W171, Rosebank Shale, *parultimus* Biozone; AMF 92349, W827, Rosebank Shale, *parultimus* Biozone. **T**, *Monograptus transgrediens* Perner, 1899, AMF 92393, W834, Cowridge Siltstone, *bouceki* Biozone. Scale bars 1 mm.

Remarks. Bulman (1928) recorded the species from the late Wenlock and Rickards *et al.* (1995) extended its range into the Ludlow (*nilssoni* Biozone). There seemed to be more variation in the specimens recorded by Rickards & Wright (1997) from the Barnby Hills Shale (*inexspectatus–kozlowskii* Biozone, late Ludlow) and, in addition to *D. elegans*, they recorded *D.* cf. *elegans* and *D. ?elegans*. The last we now feel more confident in placing with the specimens of *D. elegans* of the Barnby Hills Shale: it should be noted that the autothecal spacing of these specimens (at 20 in 10 mm) contrasts with Bulman's originals and with the Quarry Creek specimens (both 25 in 10 mm) as well as with the present material (30 in 10 mm). Thus there is no linear decrease in thecal size from the Wenlock to the late Přídolí, so *D. elegans* presently has little biostratigraphic utility in the Late Silurian. The form described as *D.* cf. *elegans* from the Barnby Hills Shale (Rickards & Wright, 1997) may yet prove to be a new species smaller than, but closely related to, *D. elegans* Bulman.

Order **Graptoloidea** Lapworth, 1875

Family **Monograptidae** Lapworth, 1873

Pristiograptus Jaekel, 1889

Type species. *Pristiograptus frequens* Jaekel, 1889, by original designation.

Pristiograptus kolednikensis Přibyl, 1940

Figs. 3E,F, 4A, 13F

1940 *Monograptus (Pristiograptus) kolednikensis* Přibyl, p. 70, text-figs. 1–8.
1943 *Pristiograptus kolednikensis* Přibyl, 1940; Přibyl, p. 20–21; text-figs. 2I,J; text-figs. 3L,M.

Material. Figured specimens AMF 92353–54 (formerly numbered University of Wollongong F1872), AMF 92365 (formerly University of Wollongong F886) and numerous other specimens (AMF 103090–94, AMF 103102, SM X.28018–22, SM X.28056–57) from localities W171, 827 and 828, *parultimus* Biozone (Přídolí), Rosebank Shale.

Diagnosis. *Pristiograptus* with sicula 2.00–2.20 mm long, apex at level of th 2 aperture; rhabdosome more or less straight; dorsoventral width 0.70–0.90 mm at level of th 1, to 1.12–1.72 mm at th 10 and up to 2.20 mm most distally; thecal spacing 11–12 in 10 mm proximally to 9–10 in 10 mm distally; thecal overlap around ½; thecal inclination 20–30°; thecal aperture of th 1 sometimes slightly rounded, but no other apertural modifications seen. Σ =1.04–1.10

Remarks. These specimens are clearly very close to *Pristiograptus fragmentalis* (Bouček, 1936) especially as recently redescribed by Koren′ & Sujarkova (1997) from the late Ludlow of south Tien Shan. They differ only in having a smaller Σ value and in having lower distal dorsoventral width (2.20 mm maximum compared with 2.2–2.8 mm). All previous descriptions of *P. fragmentalis* confirm its high dorsoventral width. Jaeger (*in* Kříž *et al.*, 1986) was of the opinion that the early growth stages of *P. fragmentalis* (and, presumably, very similar forms such as *P. kolednikensis*) were very difficult to distinguish from *P. dubius*. Whilst there is some truth in this, especially when the proximal end shows a slight ventral curvature, it seems to us that not only is the proximal end more commonly straight, but that the angle of thecal inclination of the early thecae is higher in *P. kolednikensis* and *P. fragmentalis* (contrast, for example, Figs. 3E,F and Figs. 3G–I herein; and see Koren′ & Sujarkova, 1997, text-fig. 7). Further comment on the evolution of *P. kolednikensis* is given in the evolution section. The specimen AMF 92365 is shown as Fig. 4A for direct comparison with *M. transgrediens* (Perner, 1899; Figs. 4B–E herein).

This is the first report of this species from Australia.

Pristiograptus dubius (Suess, 1851)

Figs. 3G–I

1850 *Graptolithus colonus* Barr.; Barrande, p. 43, pl. 2, fig. 5.
1851 *Graptolithus dubius* Suess, p. 115, pl. 9, figs. 5a,b.
1943 *Pristiograptus dubius dubius* (Suess, 1851); Přibyl, p. 3, pl. 1, figs. 4–6.
1958 *Pristiograptus dubius* (Suess); Urbanek, p. 83–87, text-fig. 57; pl. 5, figs. 1, 2; text-pl. 7.
1986 *Pristiograptus dubius* (Suess); Koren′, p. 119–122, pl. XXIX–XXX, text-figs. 27–29.

Material. Figured specimens (AMF 92356, 92359, 92360) all from locality W830, *praecornutus* Biozone, Black Bog Shale, late Ludlow; other specimens from the same locality are AMF 103045–52, SM X.28024–28.

Remarks. Although fitting previous descriptions fairly closely, this material exhibits some variation in sicular length from 1.40–1.88 mm. The position of the apex remains the same—midway between the apertures of th 1 and th 2—and in consequence the thecal spacing of the early thecae on those rhabdosomes with a shorter sicula is higher (15 in 10 mm compared with the more usual 12 in 10 mm; see, for example, Figs. 3G,I).

In general, *P. dubius* has been rarely illustrated or described from stratigraphic levels towards the end of its long range (early Wenlock to Přídolí); for example, it was recorded from as high as the *ultimus* Biozone (Přídolí) by Koren′ & Sujarkova (1997) but was neither figured nor described. Bearing in mind that *P. dubius* is one of the longest-ranging lineages (ranging through approximately 18 Ma) it would be useful to document its occurrences carefully. Our material shows a rather more pronounced dorsal sicular tongue (Figs. 3G–I) than do stratigraphically lower forms of *P. dubius*, but we have no way of knowing whether this is a general feature of stratigraphically high forms.

Pristiograptus shearsbyi n.sp.

Figs. 3J–P, 11A,B, 13B,E

Material. HOLOTYPE AMF 92392, locality W834, Cowridge Siltstone, Barambogie Creek, *bouceki* Biozone, Přídolí; specimen in three dimensions. PARATYPES. AMF 92385, locality W835, Rosebank Shale; AMF 92344–45, locality W827, *parultimus* Biozone, Rosebank Shale; AMF 92394–95, locality W834, *bouceki* Biozone, Cowridge Siltstone. Rare at locality W830, Black Bog Shale (AMF 92358), Ludlow. Numerous Přídolí specimens from localities W171, W827, W828, W835, Rosebank Shale; W832, W833, W834 from the Cowridge Siltstone (AMF 102956–60, 103004–12, 103017–18, 103023–25, 103095–101, 103103, SM X.27111–12, SM X.28029–31, SM X.28041–48); and from the Elmside Formation, locality W430 (AMF 102926, AMF 103053).

Etymology. After A.J. Shearsby, photographer and pioneer geologist in Yass.

Diagnosis. Straight, thin *Pristiograptus* rhabdosomes, up to 12 mm long and with a maximum dorsoventral width (flattened) of 0.85 mm; proximal dorsoventral width 0.40–0.55 mm; sicula 1.20–1.65 mm, apex reaching midway between apertures of th 1 and th 2; Σ=1.2–1.4; thecal overlap about ½; thecal inclination 10–30°; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; th 1 very rarely shows a slight rounding of the aperture; sicula with short but pronounced dorsal tongue.

Description. The proximal end is mostly quite straight, but a minority of specimens shows a very gentle ventral curvature (e.g., Figs. 3J,N,O). Occasionally, as in Fig. 3K, the apex of the sicula reaches to the level of the aperture of th 2, and it may be that the difficult-to-see prosicula usually reaches that level. The thecal overlap seems to vary slightly from just under ½ (e.g., Fig. 3J) to almost exactly ½ (Fig. 3N). The rounding seen rarely on th 1 is no more than that commonly seen in *P. dubius*, and all the thecae are essentially pristiograptid in nature. There is a very slight geniculum identifiable in some specimens (Fig. 3P) though not to the extent seen in *Pseudomonoclimacis* Mikhajlova, 1975.

Remarks. This is the first record of a slim pristiograptid from the Yass region in late Ludlow and Přídolí strata; Jaeger (1967) referred to pristiograptids of the *dubius* group from the Rosebank Shale, but not from the Cowridge Siltstone where we have found them commonly with *M. bouceki* and *M. transgrediens* on Barambogie Creek. Similarly the slender *Crinitograptus* and *Neocucullograptus* from localities W171, W827 and W828, which we describe below, have not been previously reported from these localities, although they also occur with *P. shearsbyi* n.sp. Koren′ & Sujarkova (1997) recorded *P. dubius* from as high as the *ultimus* Biozone and *P.* ex gr. *dubius* from a little higher (*tumultuosus* Biozone: they are not described or figured herein).

Other slender pristiograptids of the *dubius* group occur from the late Llandovery to the middle Ludlow. Usually they are of short duration, repeatedly arising from the stem lineage of *P. dubius*, and are difficult to distinguish one from another in view of the few available biocharacters. *Pristiograptus shearsbyi* n.sp. differs from earlier slender pristiograptids, however, in having a pronounced dorsal tongue to the sicular aperture, a feature which affects many graptoloid lineages in the late Ludlow and Přídolí. The more robust *P. dubius* (Figs. 3G–I) is similarly affected at this stratigraphic level. In lacking thickening at the base of the interthecal septum, this species is distinct from *Pseudomonoclimacis*.

Monograptus Geinitz, 1852

Type species. *Lomatoceras priodon* Bronn, 1835; subsequently designated by Bassler (1915).

Remarks. In this paper we follow the taxonomy of Koren′ & Sujarkova (1997, p. 66–67) in using a broadly-conceived *Monograptus*, arguing that recognition of genera such as *Istrograptus* Tsegelnjuk, 1988, *Scalograptus* Tsegelnjuk, 1976 and *Neocolonograptus* Urbanek, 1997 is premature: a better understanding of the evolutionary lineages is necessary before these taxa can be accepted. Although some monograptids may have arisen from a pristiograptid stock, there has been no serious suggestion that they should be referred to a taxon such as "*Pristiograptus*".

Brown & Sherrard (1952) illustrated taxa attributed to *Monograptus bohemicus* (Barrande, 1850) from portion 15, parish of Hume; this specific identification has, hitherto, remained unchallenged. To date, only Jaeger (1967) has commented again on these monograptids; he believed there were two subspecies of *Monograptus bohemicus* present through what is essentially the upper section of the Black Bog Shale covered by our localities W830 to W831. Here we distinguish three species-level taxa of curved, *bohemicus*-type graptoloids, which we identify as *Bohemograptus tenuis, B. paracornutus* n.sp. and *B. praecornutus* Urbanek, 1970. No *B. b. bohemicus sensu stricto* has been confirmed from Yass as yet, although an ample thickness of the Black Bog Shale exists below our locality W830. Further, the "*M. bohemicus*" illustrated by Brown & Sherrard (1952, see locality map fig. 1) is from just below our localities W832 and W833 on "Tulla Park", despite the fact that they did have Rainbow Hill material collected by Gordon Packham (pers. comm., GHP). The material illustrated by Brown & Sherrard (1952, fig. 2d; pl. VIII, fig. d) as *M. bohemicus* is actually *M. b. tenuis* (Fig. 12B). Our re-identifications of the names they assigned to the illustrated graptolites are given in Table 1.

Monograptus parultimus Jaeger, 1975

Figs. 3Q–S,U

1968 *Monograptus* sp., cf. *Monograptus ultimus* Perner; Packham, p. 219–220; pl. 11, figs. 1–3, 5, 6.
1975 *Monograptus parultimus* Jaeger, p. 119–125, text-fig. 44; pl. 2, figs. 4, 8.
1986 *Monograptus parultimus* Jaeger, 1975; Jaeger *in* Kříž *et al.*, p. 318–321, text-figs. 29–34; pl. 1, figs. 1, 2, 5, 8, 9; pl. 2, figs. 3–6, 23, 24; pl. 4, fig. 12.
1988 *Ludensograptus parultimus* (Jaeger, 1975); Tsegelnjuk, p. 82, fig. 5.
1990 *Pseudomonoclimacis parultimus* (Jaeger, 1975); Lenz, p. 1081, figs. J–L.
1992 *Monograptus parultimus* Jaeger, 1975; Rickards & Banks, p. 10–11, fig. 1B; pl. 1B.
1997 *Monograptus parultimus* Jaeger; Koren′ & Sujarkova, p. 78–79, text-figs. 12A–Y; pl. 4, figs. 5–12; pl. 5, figs. 1–7.

[Further references were given by Jaeger (*in* Kříž *et al.*, 1986) and Rickards & Banks (1992)]

Material. Fairly common at Přídolí localities W171, W827 and W828 (AMF 92349, AMF 92361 [formerly numbered University of Wollongong F 520], AMF 92383–84, AMF 102894, AMF 103076, SM X.28023, SM X.28049), *parultimus* Biozone, Rosebank Shale; rare at Přídolí locality W835, possibly in Přídolí localities W832–3 (AMF 103019–22), post-*parultimus* Biozone, all low in Cowridge Siltstone.

Diagnosis. *Monograptus* with rhabdosomes usually less than 10 mm long and with a maximum dorsoventral width of about 1.30 mm at that length; proximal end and sicula often with slight ventral curvature; sicula with dorsal tongue and virgella often directed at 45° to the rhabdosomal axis; thecal apertures undulating, with slight elevations, especially th 1–th 3, thereafter declining somewhat, and often with thickened rims; thecal spacing proximally 11–13 in 10 mm; distal thecal spacing 9–11 in 10 mm; thecal overlap <½; slight geniculum; base of interthecal septum often thickened; Σ=1.1–1.5; sicula 1.70–1.90 mm; dorsoventral width at th 1, 0.60–0.80 mm; dorsoventral width at th 10, 1.00–1.40 mm.

Remarks. Our material is very close to the type material from Kosov Quarry (Jaeger *in* Kříž *et al.*, 1986), but is a little different in dimensions from the specimens described recently from south Tien Shan (Koren′ & Sujarkova, 1997) which are slightly wider and have a higher Σ value. The Yass specimens are also close to the Tasmanian specimens described by Rickards & Banks (1992), differing only in having slightly more of a geniculum as, indeed, does the type material; this is almost certainly a reflection of preservational differences. Sherwin (1979, p. 161) stated that the taxon identified by Packham (1968) as *M.* cf. *ultimus* was believed to be *M. tomczyki*.

Monograptus transgrediens Perner, 1899 *sensu lato*

Figs. 3T, 4B–E, 11C, 13A

1899 *Monograptus transgrediens* Perner, p. 13, pl. 17, fig. 24.
1940 *M. (Pristiograptus) transgrediens* Perner; Přibyl, p. 68–69.
1943 *Pristiograptus transgrediens* Perner; Přibyl, p. 30–31; pl. 2, fig. 7; pl. 3, fig. 7.
1964 *M. transgrediens* (Perner); Teller, p. 52, pl. 2, fig. 3; pl. 3, figs. 1–4; pl. 7, figs. 8–12.
1982 *Monograptus transgrediens* Perner 1899; Jenkins, p. 171, fig. 3M, N(?).
?1982 *Monograptus transgrediens* cf. *praecipuus* Přibyl, 1940; Jenkins, p. 171, figs. 3G,H.
1984 *Monograptus transgrediens transgrediens* Perner, 1899; Porebska, p. 141–144, figs. 13, 1–9.
1986 *Monograptus transgrediens* Perner; Koren′, p. 115–116, text-figs. 1–6, 25; pl. 27, figs. 1–6; pl. 28, figs. 1–5.
1986 *Monograptus transgrediens* Perner, 1899; Jaeger *in* Kříž *et al.*, p. 326–328, text-figs. 41a–c; pl. 1, figs. 15, 17, 18; pl. 2, figs. 12, 16, 17, 19, 22, 25.
1990 "*Pristiograptus*" *transgrediens* (Perner); Lenz, p. 1081, figs. P–R.
1997 *Monograptus transgrediens* Perner, 1899; Koren′ & Sujarkova, p. 81–83, text-figs. 15A–P; pl. 6, figs. 3–9.
1997 *Istrograptus transgrediens transgrediens* (Perner, 1899); Teller, p. 76–77; pl. 2, figs. 1–11.

Material. Common at locality W834 (AMF 92387, AMF 92389, AMF 92390, AMF 92391, AMF 92393), low in Cowridge Siltstone, Barambogie Creek, *bouceki* Biozone, Přídolí; and a few specimens from W430 (AMF 102927a, AMF 102939–47, AMF 102966–68, SM X.27094–100), Elmside Formation, Black Range Road, *transgrediens* Biozone, Přídolí.

Diagnosis. *Monograptus* with proximal end usually with slight ventral curvature, and rounding of the thecal apertures (raised lappets) visible sometimes even on th 7, though more commonly on th 1 to th 5; sicula with slight ventral curvature, dorsal tongue, a length of 1.60–1.90 mm, Σ=1.3–1.5, and an apex which reaches to the level of between the apertures of th 1, and th 2 (though with the prosicula not often visible); proximal thecal spacing 10–13 in 10 mm, distally about 10 in 10 mm; dorsoventral width at th 1 0.70–0.80 (in three dimensions) and distally 1.30–1.50 mm (three dimensional specimens). Rhabdosomes in the Elmside Formation reaching a length of 30 mm and a dorsoventral width of 1.80 mm.

Remarks. The type material was redescribed by Jaeger (*in* Kříž *et al.*, 1986) and our material is close to that except in being shorter and hence less robust; Jaeger (*in* Kříž *et al.*, 1986) recorded a maximum length of 100 mm and a maximum width of 3 mm. Although Koren′ & Sujarkova

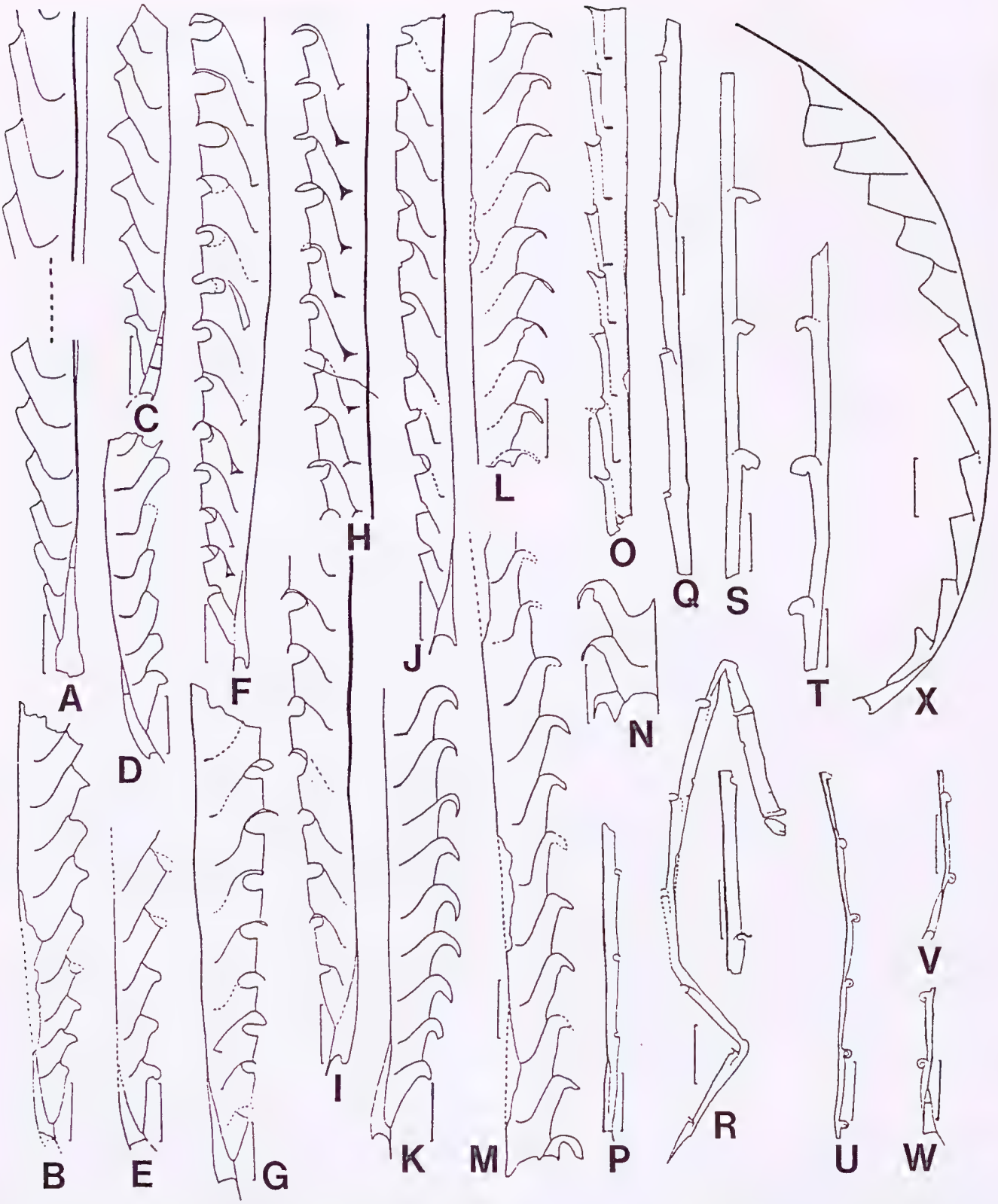

Figure 4. **A**, *Pristiograptus kolednikensis* Přibyl, 1940, AMF 92365, W171, Rosebank Shale, *parultimus* Biozone, for direct comparison with *M. transgrediens* (B–E). **B–E**, *Monograptus transgrediens* Perner, 1899, respectively AMF 92389, AMF 92391, AMF 92387, AMF 92390, W834, Cowridge Siltstone, *bouceki* Biozone. **F–I**, *Monograptus pridoliensis* Přibyl, 1981; respectively AMF 92352, AMF 92347, AMF 92351, AMF 92350, W827, Rosebank Shale, *parultimus* Biozone. **J**, *?Monograptus pridoliensis* Přibyl, 1981, AMF 92355, W171, Rosebank Shale, *parultimus* Biozone. **K–N**, *Monograptus bouceki* Přibyl, 1940, respectively, after Jaeger (1967, pl. 14, fig. A), AMF 92388, 92386, 92386b, W834, Cowridge Siltstone, *bouceki* Biozone. **O**, *Monograptus* sp. indet, AMF 102889, W834, Cowridge Siltstone, *bouceki* Biozone. **P–R**, *Crinitograptus operculatus* (Münch, 1938) respectively AMF 102891, AMF 102892, W171, Rosebank Shale, *parultimus* Biozone; and AMF 92342, W828, Rosebank Shale, *parultimus* Biozone. **S,T**, *Neocucullograptus? mitchelli* n.sp., holotype AMF 102895, W171, Rosebank Shale, *parultimus* Biozone. **U–W**, *Neocucullograptus? yassensis* n.sp., respectively AMF 92346, AMF 92344, holotype AMF 92343, W828, Rosebank Shale, *parultimus* Biozone. **X**, *Bohemograptus bohemicus tenuis* (Bouček, 1936), AMF 92339, W830, Black Bog Shale, *praecornutus* Biozone. Scale bars 1 mm.

(1997) commented on Jaeger's (*in* Kříž *et al.*, 1986) redescription of Perner's types, they did not refer to Jaeger's topotype material in their synonymy: the dimensions and form of their southern Tien Shan specimens are, however, very close to the Bohemian types. The Σ value is less in the types than either the southern Tien Shan material or the Yass material, both of which agree closely in this feature.

Monograptus transgrediens is a typical and long-ranging Přídolí species. Teller (1997) suggested that the number of beak-like thecae in "*Istrograptus*" increased gradually through the Přídolí, with "*Istrograptus*" *t. transgrediens* being typical of the highest levels with several beak-like thecae. However, our *bouceki* Biozone material has one to seven beak-like thecae, and the *transgrediens* Biozone Elmside Formation forms have far fewer, suggesting that more study of the described subspecies on a wider geographical basis is required before firm subspecific assignment can be achieved. Although Jenkins (1982) did not identify his figures 3M and 3N, we presume they represent his *M. transgrediens*. We are uncertain about the form he ascribed to *M. t.* cf. *praecipuus* (Jenkins' figs. 3G,H) and include it doubtfully in our synonymy of *M. transgrediens*. Jaeger (1967) noted that there were two forms present of *M. transgrediens* but we cannot confirm this from our material which may have a range of sizes from smaller earlier growth stages to "normal" late growth stages.

Monograptus pridoliensis Přibyl, 1981

Figs. 4F–I,?J, 13D

1940 *Monograptus (Pomatograptus) similis* Přibyl, p. 72, text-figs. 1, 3; pl. 1, fig. 5.
1981 *Monograptus pridoliensis* nom. nov.; Přibyl, p. 371–372, text-figs. 1, 3–6; pl. 1, fig. 1; pl. 2, fig. 6.
1986 *Monograptus pridoliensis* Přibyl, 1981; Jaeger *in* Kříž *et al.*, p. 328–330, text-fig. 42; pl. 3, figs. 1, 12; pl. 4, figs. 2, 3, 8, 9, 11.
1990 *Monograptus* cf. *pridoliensis* Přibyl; Rickards & Garratt, p. 43–44, figs. 4a–f.

Material. Numerous specimens from localities W171, W827, W828 (AMF 92347–48, AMF 92350–51, AMF 92352, ?AMF 92355 (formerly University of Wollongong F 1872), AMF 103077–89, SM X.28052–55), *parultimus* Biozone, Rosebank Shale, Přídolí.

Diagnosis. *Monograptus* with more or less straight rhabdosome but with dorsal margin showing slight ventral curvature over the first few thecae; sicula effectively straightens the rhabdosome outline, even giving a slight dorsal flexure (Fig. 4F) in some specimens; sicula 1.50–2.0 mm long; Σ=1.2–1.5; sicular apex almost to level of second thecal aperture; dorsal sicular tongue; slight ventral curvature of sicula common; thecae with pronounced hoods which lessen a little distally; thecal overlap about ½ proximally, base of interthecal septum being above the level of the preceding aperture, increasing distally to more than ½; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; dorsoventral width proximally 0.65–0.80 mm; at th 10 is 1.40–1.70 mm and most distally is 2.00 mm.

Remarks. Our material so closely resembles that described by Rickards & Garratt (1990) as *M.* cf. *pridoliensis*, from the Přídolí part of the Humevale Formation of Victoria, that we include the latter in synonymy with *M. pridoliensis*. At most, the only difference is the very slightly more slender proximal end of the Yass material (0.65–0.80 mm compared with 0.70–0.90 mm at the level of th 1). From the type material redescribed by Jaeger (*in* Kříž *et al.*, 1986) our material differs only in having the hood slightly less developed.

In Bohemia *M. pridoliensis* is recorded only from the eponymous biozone, above that of *lochkovensis*, whereas our material is unquestionably from the earlier *parultimus* Biozone. Koren′ (1983), however, recorded *M. similis* from the *formosus* Biozone of Kazakhstan, so our record from Yass is not stratigraphically out of place in a global sense; this Kazakhstan material has been redescribed as *M. bessobaensis* Koren′, 1986. The differences between *M. pridoliensis* and other similar species such as *M. prognatus* Koren′, 1983 were discussed by Koren′ (1983) and Rickards & Garratt (1990) and will not be repeated here, but the evolutionary possibilities of the form are outlined in the section on evolution.

Monograptus bouceki Přibyl, 1940

Figs. 4K–N, 12A, 13C

1937 *Monograptus flemingii* (Salter); Sherrard & Keble, p. 313, pl. XV, figs. 4, 5, text-figs. 20–22.
1940 *Monograptus (Pomatograptus) bouceki* Přibyl, p. 71, text-fig. 1, pl. 1, figs. 7, 8.
1952 *Monograptus salweyi* (Hopkinson); Brown & Sherrard, p. 132, pl. VIII, figs. a,b; text-figs. 2b,c.
1967 *Monograptus bouceki* Přibyl; Jaeger (not described), pl. 14A.
1986 *Monograptus bouceki* Přibyl, 1940; Jaeger *in* Kříž *et al.*, p. 331–332, pl. 3, figs. 3, 7–11, 13, 15.
1986 *Monograptus bouceki* Přibyl, 1940; Koren′, p. 97–99, pl. XX, figs. 2–4; text-fig. 15.
1997 *Monograptus bouceki* Přibyl, 1940; Koren′ & Sujarkova, p. 71–73, text-fig. 9B–D,I–L; pl. 1, fig. 8; pl. 2, figs. 1–9.
1997 *Monograptus bouceki* Přibyl, 1940; Koren′ (*in* Nikitin & Bandaletov), p. 97–99, pl. 20, figs. 2–4; text-fig. 15.

[Fuller synonymies are given in Jaeger (*in* Kříž *et al.*, 1986) and in Koren′ & Sujarkova (1997)]

Material. Numerous specimens from locality W834, *bouceki* Biozone, Cowridge Siltstone, Barambogie Creek (AMF 92386, AMF 92388), Přídolí. We have restudied AMF 44608, the specimen illustrated as *Monograptus salweyi* (Hopkinson) by Brown & Sherrard (1952, pl. VIII, fig. b); it is re-illustrated here (Fig. 12A), but does

not appear to be a specimen illustrated by Sherrard & Keble (1937).

Diagnosis. *Monograptus* with more or less straight rhabdosome, but often with a slight dorsal flexure proximally caused largely by the position of the sicula (Fig. 4K); sicula 1.65 mm long (seen, but possibly incomplete); Σ=1.3; apex of sicula below level of hood of th 2; sicula with ventral curvature; dorsal tongue present; proximal dorsoventral width 0.90–1.10 mm; distal dorsoventral width up to 1.50–2.00 mm; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; thecae claw-like in profile with strong development of dorsal thecal wall only; thecal overlap always ½ or less; thecal inclination 35–40°.

Remarks. The Yass material seems to differ from the types only in being a little more slender throughout; indeed Jaeger's (1967) original figure (pl. 14, fig. A: reproduced herein as Fig. 4K) was also of a slightly slender form. Material described by Koren′ & Sujarkova (1997) is a little more robust, but is otherwise identical. *Monograptus bouceki* appears in the eponymous biozone and ranges higher, just into the *transgrediens* Biozone at the top of the Přídolí (Jaeger, *in* Kříž *et al*., 1986).

Monograptus formosus Bouček, 1931b

Monograptus formosus jenkinsi n.subsp.

Figs. 11M,N, 13J

1982 *Monograptus* cf. *formosus* Bouček, 1931b; Jenkins, p. 171, fig. 3E.

Material. HOLOTYPE, ANU 35910, only specimen as part and counterpart, from the Elmside Formation, Black Range Road, NW of Yass (see Jenkins, 1982, p. 167); *transgrediens* Biozone, late Přídolí.

Etymology. For Dr C.J. Jenkins, who first described this specimen.

Diagnosis. *Monograptus formosus* with slender rhabdosome no more than 0.88 mm in dorsoventral width; thecal spacing of 8–9 in 10 mm; thecal hook occupying about one half the rhabdosomal width; dorsal thecal wall strongly retroverted, pointing almost dorsally at its distal extremity; free ventral wall inclined at about 15°; thecal overlap very low, less than one sixth.

Remarks. The new subspecies differs from the type subspecies not only in being half as wide but also in having the prothecal wall inclined at a lower angle throughout the rhabdosome (15° compared with 20–30°), in having less thecal overlap (compare Figs. 11M,N with 11K,L) and in having a lower thecal height (up to 1.30–1.40 mm in the type subspecies). The thecal spacing of *M. f. jenkinsi* n.subsp. is identical with that of the type subspecies as described by Jaeger (1967) and Packham (1968) from the Rosebank Shale (Figs. 11J–L herein). The nature of the thecal hooks (not lappets) appears to be the same in both taxa except that they are wider and higher in the type subspecies. *Monograptus uncatus* Koren′ & Sujarkova, 1997 has similar width and comparable thecal spacing.

This is the only occurrence of this species at Yass, other than the stratigraphically lower occurrence in the *formosus* Biozone (Jaeger, 1967; Packham, 1968) which is, as stated above, late Ludlow to earliest Přídolí.

Monograptus hornyi Jaeger (*in* Kříž *et al*., 1986)

Figs. 11D–G, 13G

1982 *Monograptus* cf. *angustidens* Přibyl, 1940; Jenkins, p. 169–170, figs. 3F,I–L,O–Q.

1986 *Monograptus hornyi* Jaeger; *in* Kříž *et al*., p. 330–331, pl. 3, figs. 2, 6: pl. 4, figs. 16–17.

Material. Numerous well preserved specimens, many in three dimensions, from the Elmside Formation, W430, Black Range Road, *transgrediens* Biozone, Přídolí. Figured specimens AMF 102920–21, AMF 102923–24; other specimens are SM X.27113–17 and AMF 102922, AMF 102948–55, AMF 103002–03.

Diagnosis. *Monograptus* with rhabdosome up to 5.5 cm long with a maximum, distal, dorsoventral width of 2.20 mm; proximal end with characteristic gentle dorsal flexure affecting up to 7 thecae, occasionally almost straight; sicula emphasizes dorsal curvature of rhabdosome, but itself is often with strong ventral curvature, so that the extremely robust virgella points proximoventrally; sicula 1.30–1.65 mm long (mean 1.58), apex reaching above the level of the hood of th 1, sometimes to the level of the hood of th 2; thecae strongly hooked and claw-like throughout; overlapping at most ½ half distally; spaced at 12–15 in 10 mm proximally and 9–10 in 10 mm distally; thecal hook is a dorsal hood with little or no growth of the ventral apertural margin; some lateral expansion of the hood is likely; Σ=1.2 mm.

Remarks. Jenkins (1982) placed specimens from this locality in the *M. angustidens–M. uniformis* group, but the mesial and distal thecal overlap of ½ in *M. hornyi* preclude reference to *M. uniformis* as thecal overlap is much greater in the Lower Devonian species group. *Monograptus bouceki* is the most closely-related species, but *M. hornyi* has a shorter sicula: 1.5–1.8 mm in the type locality, 1.4–1.6 mm in the Elmside locality, compared with 1.80–2.22 mm in *M. bouceki* (Jaeger *in* Kříž *et al*., 1986; Koren′ & Sujarkova, 1997). The Σ values are also lower in *M. hornyi* (1.2 at Elmside; 1.2–1.3, usually, in the type material, compared with 1.2–1.6 in *M. bouceki*). The characteristic proximal curvature of the Elmside specimens contrasts with straighter rhabdosomes of *M. bouceki* from locality W834 (Fig. 2) but specimens of *M. bouceki* described by Koren′ &

Sujarkova (1997) from South Tien Shan do show similar curvature to *M. hornyi* from the Elmside Formation. The known stratigraphical ranges of *M. bouceki* and *M. hornyi* are, respectively, *bouceki* to *transgrediens* biozones and *lochkovensis* to *perneri* biozones; further documentation of these rarely recorded species may establish their morphological and evolutionary limits. *Monograptus hornyi* differs from *M. pridoliensis*, which we also describe from the Yass district in that the latter has less retroverted hoods so that the ventral thecal wall is commonly visible and the hooks appear more beak-like than hooked, especially distally. *Monograptus prognatus* Koren′, 1983 has much greater thecal overlap than *M. hornyi*, already apparent by th 15. The Elmside specimens reach a greater dorsoventral width than in Jaeger's (*in* Kříž *et al.*, 1986) type material, but the latter are shorter rhabdosomes: at comparable lengths the dorsoventral width is the same. The robust virgella seen in the Elmside specimens is a feature of old age and thus is not seen in the type material which only rarely reaches 30 mm long (usually less than 20 mm).

Monograptus perneri Bouček, 1931a

Monograptus perneri elmsidensis n.subsp.

Figs. 11H,I, 13H,I

Material. HOLOTYPE AMF 102922 (part and counterpart) and PARATYPE AMF 103001 both from locality W430, Elmside Formation, Black Range Road, *transgrediens* Biozone, late Přídolí.

Etymology. This subspecies takes its name from the nearby property Elmside (Fig. 1).

Diagnosis. *Monograptus perneri* with unusually narrow rhabdosome, no more than 0.75 mm dorsoventral width, and a slightly straighter rhabdosome than *M. p. perneri* Bouček, 1931a or *M. p. kasachstanensis* Mikhajlova, 1975 but still with dorsal curvature; thecal spacing 10–11 in 10 mm; thecal overlap about a half; thecal hook occupies a third of overall rhabdosomal width; thecal hook retroverted, seemingly pointing proximally; sicula 1.80 mm long, with ventral curvature, apex reaching midway between the apertures of th 1 and th 2, short dorsal process, small virgella; Σ=1.44 mm.

Remarks. *Monograptus perneri elmsidensis* n.subsp. is straighter and conspicuously narrower than *M. p. perneri* and *M. p. kasachstanensis* Mikhajlova, 1975 whilst retaining the overall rhabdosomal aspect and thecal style. The thecal spacing is lower than the other subspecies and the Σ value greater; because of the thin rhabdosome, the interthecal septa are almost parallel to the axis. We have found only the two specimens amongst several hundred graptolites collected at the locality, so it must be considered a rare component of the fauna.

Monograptus sp. indet.

Fig. 4 O

Material. One specimen lacking a proximal end, in full profile and three dimensions, AMF 102889, from locality W834, *bouceki* Biozone, Přídolí. Cowridge Siltstone, Barambogie Creek.

Remarks. This striking specimen has low-angled thecae with an overlap around ½ thecal apertures with thickened lips, and a similarly thickened base to the interthecal septum. It seems to resemble none of the described species at this level, nor any in the late Ludlow. There is a slight geniculum, but apparently no hood, and the ventral apertural lip may be slightly denticulate. It may represent the distal thecae of a biform species. *Monograptus balticus* Teller, 1966 has similar dimensions in its distal thecae but our form has less overlap and lacks thecal hoods; *Monograptus microdon aksajensis* Koren′, 1993 is closer on thecal overlap but this form has thecal hoods on its distal thecae.

Crinitograptus Rickards, 1995

Type species. *Monograptus crinitus* Wood, 1900, by original designation.

Crinitograptus operculatus (Münch, 1938)

Figs. 4P–R

1938 *Barrandeograptus operculatus* Münch, p. 53–68, text-figs. 2a–c; pl. 8, figs. 1, 2, 5, 6, 11; pl. 9, figs. 4, 5.

non 1952 *Monograptus crinitus* Wood; Brown & Sherrard, p. 132–133, text-fig. 2a.

?1955 *Barrandeograptus operculatus* (Münch); Kühne, p. 397–399, figs. 18A–F.

1995 *Crinitograptus operculatus* (Münch); Rickards, fig. 3.2.

Material. Fairly common at localities W171, W827, W828 (AMF 92342, AMF 102891–93, AMF 103104–06, SM X.28032–39), *parultimus* Biozone, Přídolí. Rosebank Shale.

Diagnosis. *Crinitograptus* of typically slender dimensions and fragile appearance, maximum dorsoventral width 0.40 mm, proximally 0.25–0.28 mm; sicula 1.20 mm long; apex well below level of aperture of th 1; Σ=1.7; sicular aperture without noticeable tongue; thecal apertures small, semi-circular excavations with a genicular hood and slightly undulating lateral and ventral margin; thecal overlap obscure, but may be small; proximal thecal spacing 7 in 10 mm falling to 4 in 10 mm most distally; thecae uniform; thecal inclination almost 0°; nema conspicuously more sclerotised than remainder of colony; virgella tiny.

Remarks. Rickards (1995) placed this species in synonymy with the type species *C. crinitus*, but they are here considered

distinct. In the latter the thecal spacing is closer distally (5 in 10 mm proximally, 7 in 10 mm distally) whereas the reverse is true in *C. operculatus*, and the thecal spacing is lower. *Crinitograptus crinitus* is typically a low Ludlow species and *C. operculatus* a Přídolí form in the Yass area. This is the first report of the genus from Australia.

Brown & Sherrard (1952, p. 132, text-fig. 2e) described a specimen (AMF 44615) from one (not specified) of their "*M. bohemicus*" localities as *Monograptus crinitus* Wood. This specimen is less slender and has quite different cited thecal spacings to those seen in our specimens; we conclude that the material represents proximal portions of *Linograptus p. posthumus* which occurs commonly at the "*M. bohemicus*" level.

Neocucullograptus Urbanek, 1970

Type species. *Neocucullograptus kozlowskii* Urbanek, 1970, by original designation.

Remarks. Two forms are described tentatively (perhaps temporarily) under this genus as no other genus appears to be an appropriate place for them. They show neocucullograptine features including the proximal end and possibly typical thecal hooks, but are distinct in their tiny dimensions; in the rock they are inconspicuous in the extreme and might easily be overlooked in the field.

Neocucullograptus? yassensis n.sp.

Figs. 4U–W, 13L,M

Material. HOLOTYPE AMF 92343, locality W828. PARATYPES AMF 92344 (locality W828) and AMF 92346 (locality W827). Both localities *parultimus* Biozone, Přídolí, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek.

Etymology. After the Yass district of New South Wales.

Diagnosis. Minuscule neocucullograptid rhabdosome with a dorsoventral width ranging from 0.20–0.24 mm, more or less straight; sicula 0.75 mm extending about half way along th 1; possible dorsal process; Σ=1.10–1.25; thecae with "hooks" of unknown structure; thecal spacing 7–9 in 10 mm close to the proximal end, 9–10 in 10 mm more distally; free ventral wall almost parallel to rhabdosomal axis with small amount of late prothecal expansion; thecal overlap small, but not clear; thecal "hook" occupying about half the rhabdosomal width; dorsoventral width immediately prior to "hook" is 0.10–0.12 mm.

Remarks. Although the proximal end looks like described neocucullograptines it is much smaller and narrower, with a sicula only half the length of that of *N. inexspectatus* Urbanek, 1970 and only one third that of *N. kozlowskii* Urbanek, 1970. We can equate *N.? yassensis* with no other species group at present; its proper generic attribution must remain in doubt until more material is available.

Neocucullograptus? mitchelli n.sp.

Figs. 4S,T

Material. HOLOTYPE, AMF 102895 (part and counterpart), locality W171, *parultimus* Biozone, Přídolí, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek.

Etymology. After John Mitchell, pioneer geologist in the Yass district.

Diagnosis. Minuscule neocucullograptine rhabdosome with dorsoventral width of 0.50–0.70 mm including "hook"; excluding hooks the parallel-sided metathecal part has a width of only 0.20–0.30 mm; proximal end not known, but thecal spacing constant at 4.5 in 10 mm; thecal overlap obscure, probably small; thecal inclination 0°; thecal hook occupies about half the rhabdosome width; thecal "hook" obscure, apparently facing ventrally.

Remarks. This species is quite unlike any previously-described form in the Ludlow or Přídolí. The thecal "hooks" are quite unlike the apertural hoods in *Crinitograptus*, and are different from the possibly enrolled "hooks" in *N.? yassensis* n.sp. Both *N.? yassensis* n.sp. and *N.? mitchelli* n.sp. **may** have the neocucullograptine style of apertural processes but this is not certain.

Bohemograptus Přibyl, 1967

Type species. *Graptolithus bohemicus* Barrande, 1850, by original designation.

Bohemograptus praecornutus Urbanek, 1970

Figs. 5C–L, 13K

1970 *Bohemograptus praecornutus* Urbanek, p. 301–310, text-fig. 16; pl. 20C; pls 23, 24.
1976 *Bohemograptus arcuatus* Tsegelnjuk, p. 128, pl. 40, figs. 6–9.
?1976 *Bohemograptus urbaneki* Tsegelnjuk, p. 129, pl. 40, figs. 10–12.
1990 *Bohemograptus praecornutus* Urbanek; Lenz, figs. 3Q,R.
1995 *Bohemograptus praecornutus* Urbanek, 1970: Štorch, p. 71–72, text-figs. 3C,I; text-figs. 4A,E,G; pl. 1, fig. 4; pl. 3, figs. 4, 7.
1997 *Bohemograptus praecornutus* Urbanek; Urbanek & Teller, pl. 4, fig. 9.

Material. Numerous specimens from locality W830, *praecornutus* Biozone, late Ludlow, Black Bog Shale, Rainbow Hill, AMF 92303, AMF 92331–34, AMF 92336–38, AMF 102898, AMF 103026–36, AMF 103171–72; SM X.28050–55.

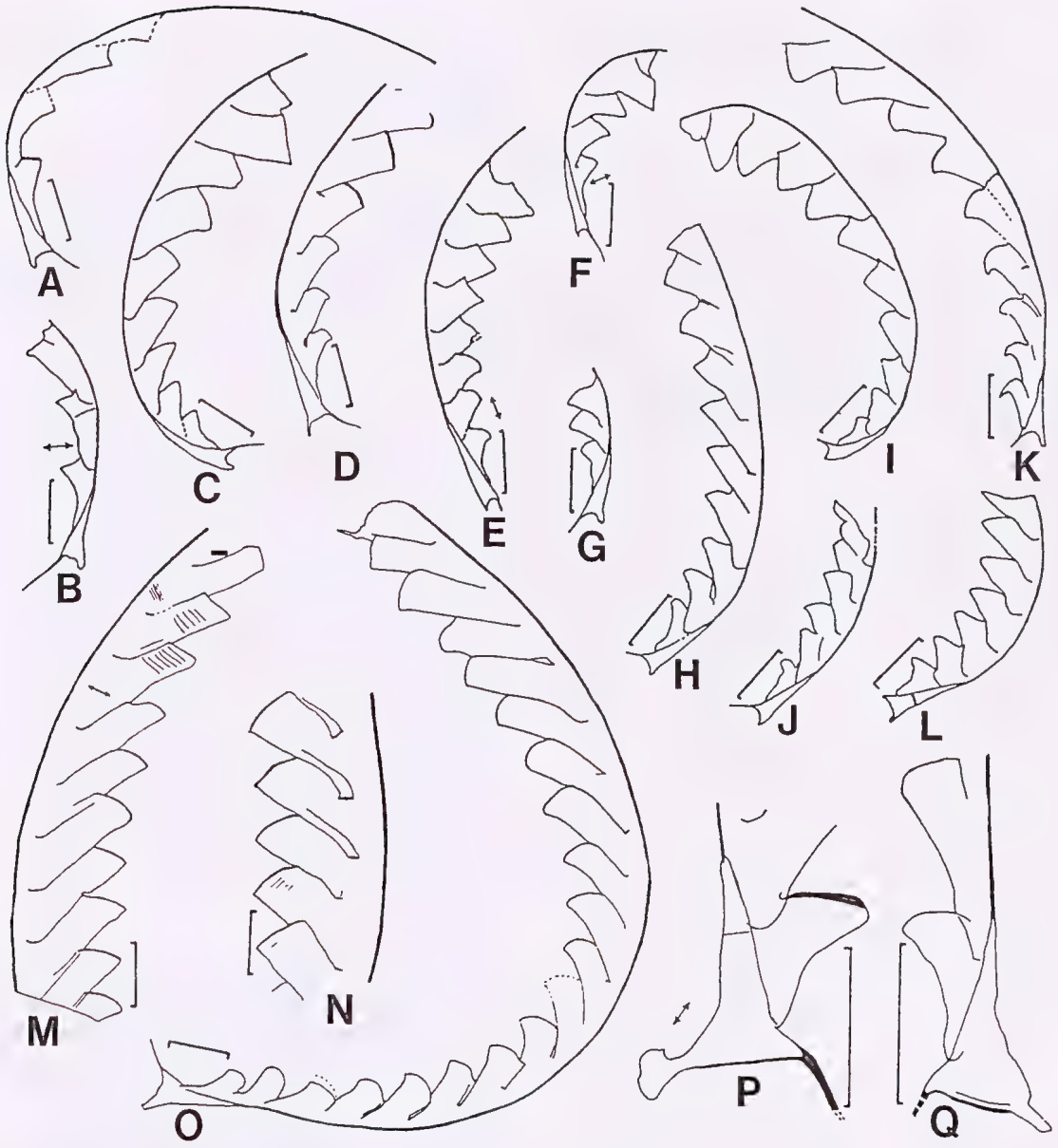

Figure 5. **A,B**, *Bohemograptus bohemicus tenuis* (Bouček, 1936), respectively AMF 92341, AMF 92340, both W830, Black Bog Shale, *praecornutus* Biozone. **C–L**, *Bohemograptus praecornutus* Urbanek, 1970, respectively AMF 92334, AMF 102898, AMF 92338, AMF 92335, AMF 92332, AMF 92331, AMF 92337, AMF 92333, AMF 92303, AMF 92336, all W830, Black Bog Shale, *praecornutus* Biozone. **M–Q**, *Bohemograptus paracornutus* n.sp., respectively AMF 92323, AMF 92311, AMF 92324, AMF 92322, AMF 92302, all W831, top of Black Bog Shale, *cornutus* Biozone. D, K and L show the maximum apertural widening seen in *B. praecornutus*. Scale bars 1 mm.

Diagnosis. *Bohemograptus* with tight ventral curvature and relatively robust rhabdosome with a distal dorsoventral width of up to 1.40 mm at 10 mm from the sicula; dorsoventral width at th 1, 0.45–0.70 mm, at th 10, 0.80–1.30 mm; sicula 1.10–1.50 mm; apex midway between apertures of th 1 and th 2; sicula straight or ventrally curved, with pronounced dorsal tongue directed dorsally; proximal thecal spacing 12–18 in 10 mm; distal thecal spacing as low as 10 in 10 mm; most thecal apertures rounded or with undulating margins; proximal thecae often slightly isolated in profile; thecal overlap about ½ throughout; thecal inclination 40–50°.

Remarks. The sicular length is closer to Urbanek's (1970) type material than to Štorch's (1995) recent description of Bohemian specimens, but our material partly overlaps with both. Otherwise the material is very close to previous descriptions on all counts. One specimen (Fig. 5K) may have the veliger morph features recorded by Urbanek (1970) but is not well preserved; it is the only one possibly showing such features. The differences from *B. paracornutus* n.sp. are discussed under the following description. This is the first report of the species from Australia. Dr T. Koren′ (pers. comm.) has informed us that *B. urbaneki* Tsegelnjuk, 1976 differs from *N. praecornutus*

Urbanek in having a larger sicula with a higher position of the apex, smaller dorsoventral width and weaker gradient of rhabdosomal widening.

Bohemograptus paracornutus n.sp.

Figs. 5M–Q, 6A–N, 7, 9A,B, 10A–E

Material. HOLOTYPE AMF 92317. Figured PARATYPES AMF 92301–02, AMF 92305–08, AMF 92311, AMF 92319–30, AMF 92363–64; other specimens among the available thousands include: AMF 102969–103000, AMF 103054–75, SM X.27178–242. All from from *cornutus* Biozone, late Ludlow, topmost Black Bog Shale, Rainbow Hill, locality W831.

Etymology. This name draws attention to the similar precursor *B. praecornutus*.

Diagnosis. *Bohemograptus* of relatively robust proportions, with strong ventral curvature so that rhabdosomes are approximately semicircular with the thecae on the inside (Fig. 6A,B). Sicula with spectacular apertural expansion so that the sicula is trumpet-shaped; length 1.36–1.52 mm; apex reaching mid way between the th 1 and th 2 apertures; apertural width 0.90–1.50 mm; prosicula about 0.50 mm; metasicular expansion begins sharply when the sicula is about half grown; dorsal sicular lip with pronounced, often winged, process, directed dorsally, proximally or (rarely) ventrally; rest of sicular aperture (the lateral margins) convexly curved, and strongly thickened; virgella robust, spike-like, directed proximoventrally, up to 1 mm long. Dorsoventral width at th 1, 0.60–1.00 mm; at th 5, 0.90–1.30 mm; and most distally up to 2.00 mm; proximal thecal spacing 12–16 in 10 mm, distally 10–12 in 10 mm; th 1 with markedly concave free ventral wall; subsequent thecae have more or less straight free ventral wall inclined at 40–60°, sometimes slightly concave below the apertures; thecal apertures rounded or undulating, thickened, with lateral elevations with arched fuselli; thecal overlap < ½ proximally and > ½ distally; Σ=1.00–1.28.

Remarks. *Bohemograptus paracornutus* n.sp. is clearly very close to *B. praecornutus*, which it resembles in rhabdosome size, shape, thecal type and thecal spacing, and in the position of the apex of the sicula. Both can be contrasted in this last aspect with *B. b. tenuis*, in which the sicular apex is **below** the level of the aperture of th 1 and the whole proximal end is slim rather than robust. *Bohemograptus paracornutus* n.sp. differs from *B. praecornutus* in its spectacularly expanded sicula. All the specimens we have, numbering in the thousands, show this feature; and of all the specimens of *B. praecornutus* we have examined from locality W830 none has an expanded sicular aperture, Figs. 5K,L being the only specimens showing a very slight expansion. The evolutionary relationship of *B. paracornutus* n.sp. to *B. praecornutus* is discussed in the earlier section on evolution of the Yass fauna. *Bohemograptus paracornutus* n.sp. differs from *B. paratenuis* n.sp. (proposed below) in that the latter has the *B. b. tenuis* style of proximal end, that is rather slim and with the apex of the sicula below the level of the aperture of th 1 and thecae inclined at a much lower angle (20°; see Fig. 4X, Figs. 5A,B).

The NSW geological literature is replete with references to *Monograptus bohemicus* or *Bohemograptus bohemicus* from Yass, mostly simply following Brown & Sherrard (1952) and not being based (in many cases) on actual specimens; it is impossible to speculate on the veracity of these records. However, material illustrated by Brown & Sherrard (1952) is here assigned to *B. b. tenuis*.

Bohemograptus paratenuis n.sp.

1970 *Bohemograptus bohemicus* aff. *tenuis* Bouček, 1936); Urbanek, p. 299, pl. 19.

Material. HOLOTYPE: we nominate the un-numbered specimen in Urbanek (1970, Plate XIX, figure A) as holotype. PARATYPES: five specimens figured by Urbanek (1970, plate XIX, figs. B, C, D, E and F). All material figured by Urbanek in Plate XIX is from the erratic boulder S. 234, Mochty, Poland. The repository is the Palaeozoological Laboratory, Warsaw University. The type material was examined by Rickards in 1986.

Etymology. To indicate relationship to *Bohemograptus b. tenuis* (Bouček, 1936), as discussed in the biostratigraphy and evolution section.

Diagnosis. *Bohemograptus* with trumpet-shaped sicula, the apex of which is located below the level of the aperture of th 1, or no higher than it: angle of free ventral wall of th 1, 10–20°, gently concave; origin of th 1 well above the sicular aperture (0.30–0.35 mm); several metasicular thickened bands, one on the pro/metasicular boundary; pseudo-microfusellar additions to thecal apertures; sicular aperture 0.60–0.70 mm with pronounced and winged dorsal process, directed dorsally or proximally; Σ=1.46–1.56.

Remarks. As suggested by Urbanek, this species is close to *Bohemograptus b. tenuis* (Figs. 5A,B, 4X) but shows the same morphological relationship to that species as *B. paracornutus* n.sp. does to *B. praecornutus*, namely the development of a trumpet-shaped sicular aperture. *Bohemograptus paratenuis* n.sp. differs from *B. paracornutus* n.sp. and *B. praecornutus* in having the origin of th 1 much farther away from the sicular aperture, in the much lower angle of inclination of the free ventral wall of th 1, in the greater Σ value, and in the more proximal position of th apex of the sicula. The trumpet shaped sicula is also narrower than in *B. paracornutus* n.sp.

Egregiograptus Rickards & Wright, 1997

Type species. *Monograptus egregius* Urbanek, 1970; by original designation.

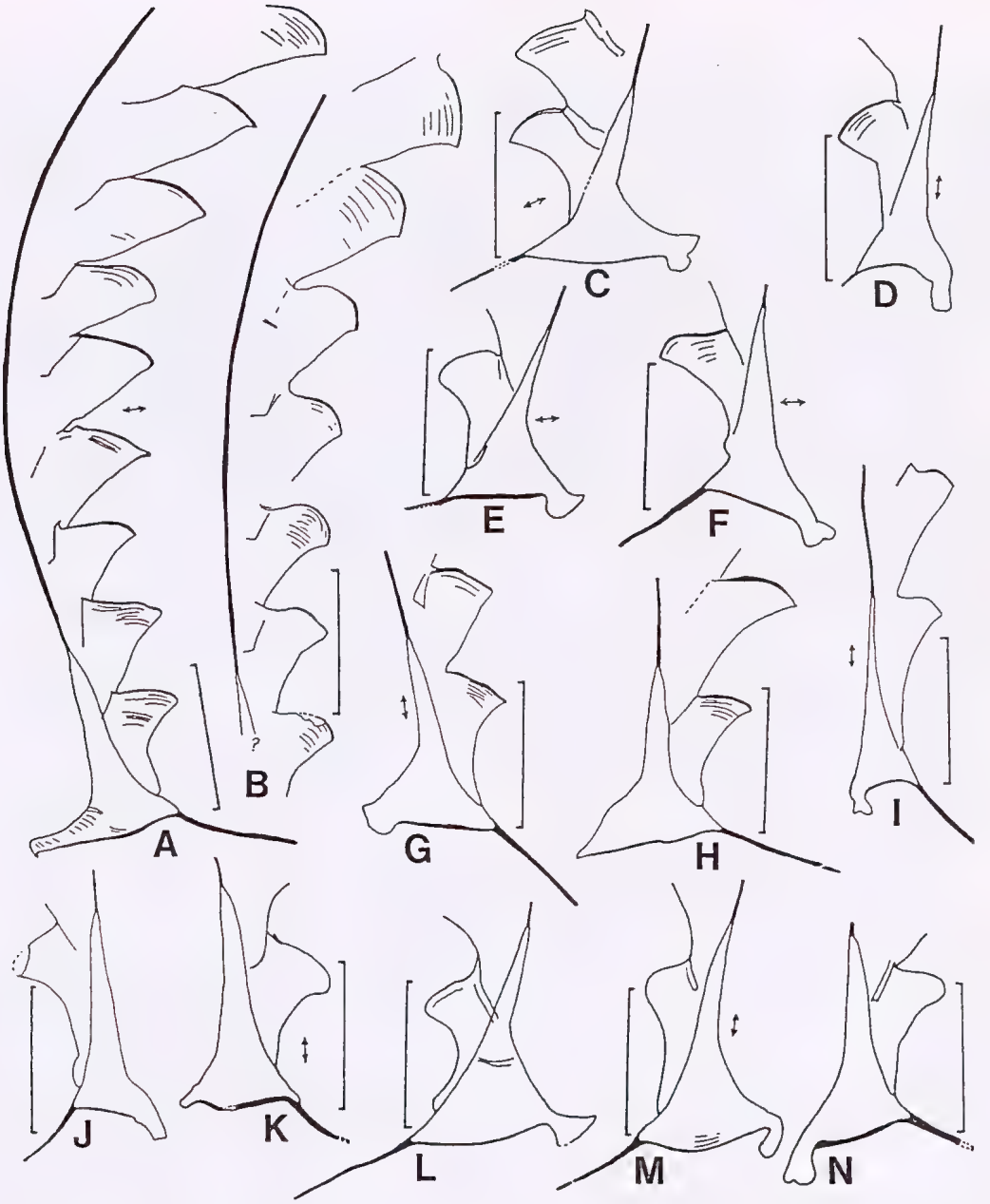

Figure 6. A–N, *Bohemograptus paracornutus* n.sp., respectively AMF 92306, AMF 92305, AMF 92328, AMF 92308, AMF 92326, AMF 92307, AMF 92320, AMF 92319, AMF 92321, AMF 92301, AMF 92325, AMF 92330, AMF 92327, AMF 92329, all W831, top of Black Bog Shale, *cornutus* Biozone. Scale bars 1 mm; tectonic stretching indicated by arrows, where appropriate.

Egregiograptus sp. indet.

Fig. 12C

Material. AMF 44614.

Remarks. Brown & Sherrard (1952, pl. VIII, fig. g) illustrated graptolites on a small slab as *Monograptus roemeri* (Barrande). Most of the specimens are here identified as *Bohemograptus bohemicus tenuis*, but one fragmentary specimen is here assigned to *Egregiograptus*. Sherwin (1979, p. 161) referred this material to the Barrandian species *M. butovicensis*; this species is the type species of *Polonograptus* Tsegelnjuk, 1976, which is a genus that must yet be used with caution (Urbanek & Teller, 1997; Rickards & Wright, 1999) as the type species is poorly known.

Linograptus Frech, 1897

Type species. *Dicranograptus posthumus* Richter, 1875; by original designation.

Figure 7. *Bohemograptus paracornutus* n.sp., holotype AMF 92317, W831, top of Black Bog Shale, *cornutus* Biozone.

Remarks. The type subspecies, *Linograptus p. posthumus* (Fig. 8A–C), ranges at Yass from high in the Black Bog Shale in the *cornutus* Biozone to the Přídolí lower part of the Elmside Formation, where it occurs locally in high abundance (Fig. 2). *Linograptus posthumus introversus*, described by us from the late Ludlow Barnby Hills Shale near Wellington, occurs at Yass at collection level 3 (Fig. 8D), a few metres higher than the lowest occurrence of the type subspecies as reported by Brown & Sherrard (1952) as *Monograptus crinitus* (see above under *Crinitograptus*).

Graptolite biostratigraphy

Figure 2 shows the ranges of the Yass graptolites plotted against the established lithostratigraphy, chronostratigraphy and biostratigraphy. Earlier records, such as those of Jaeger (1967), Packham (1968) and Jenkins (1982) are included but not records of out-of-date names in the form of previous identifications, which are listed in Table 1. Most of the species we have listed in Fig. 2 are new records and include several new species. Twenty-seven taxa are recognised, compared with the sparse faunas previously recognised for the Yass area. It is important to recognise that we have not collected through numerous stratigraphic sections, as this is precluded by the exposures: rather, we have collected from mostly previously recognised localities which are well-controlled stratigraphically, as shown on Fig. 1. Placement within a Biozone is not possible in the Yass district occurrences, particularly in view of the discontinuous nature of the graptolite record.

The stratigraphically lowest reported graptolites are all dendroids from the Barrandella Shale Member of the Silverdale Formation in the Yass district and include: those mentioned by Jaeger (1967) from low in the unit; Shearsby's (1912) earlier report; and *Dictyonema* sp. cited by Cramsie *et al.* (1978) from low in the member at Hattons Corner. In a late stage of the preparation of this manuscript, *Dictyonema sherrardae mumbilensis* Rickards & Wright, 1997 was collected from the member in the Yass River upstream from Hattons Corner; we have not seen any dendroid material noted by other authors (Shearsby, 1912; Jaeger, 1967; Cramsie *et al.*, 1978).

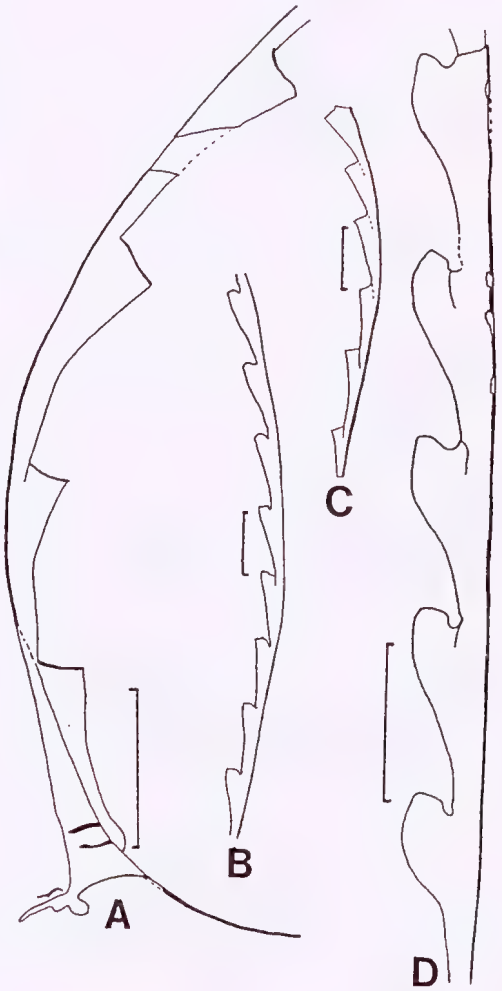

Figure 8. **A–C**, *Linograptus posthumus posthumus* Richter, 1875, respectively AMF 92314, W830, Black Bog Shale, *praecornutus* Biozone; AMF 102897, W171, Rosebank Shale, *parultimus* Biozone; AMF 92367, W830, Black Bog Shale, *praecornutus* Biozone. **D**, *Linograptus posthumus introversus* Rickards & Wright, 1997, AMF 92304, W831, top of Black Bog Shale, *cornutus* Biozone. Scale bars 1 mm.

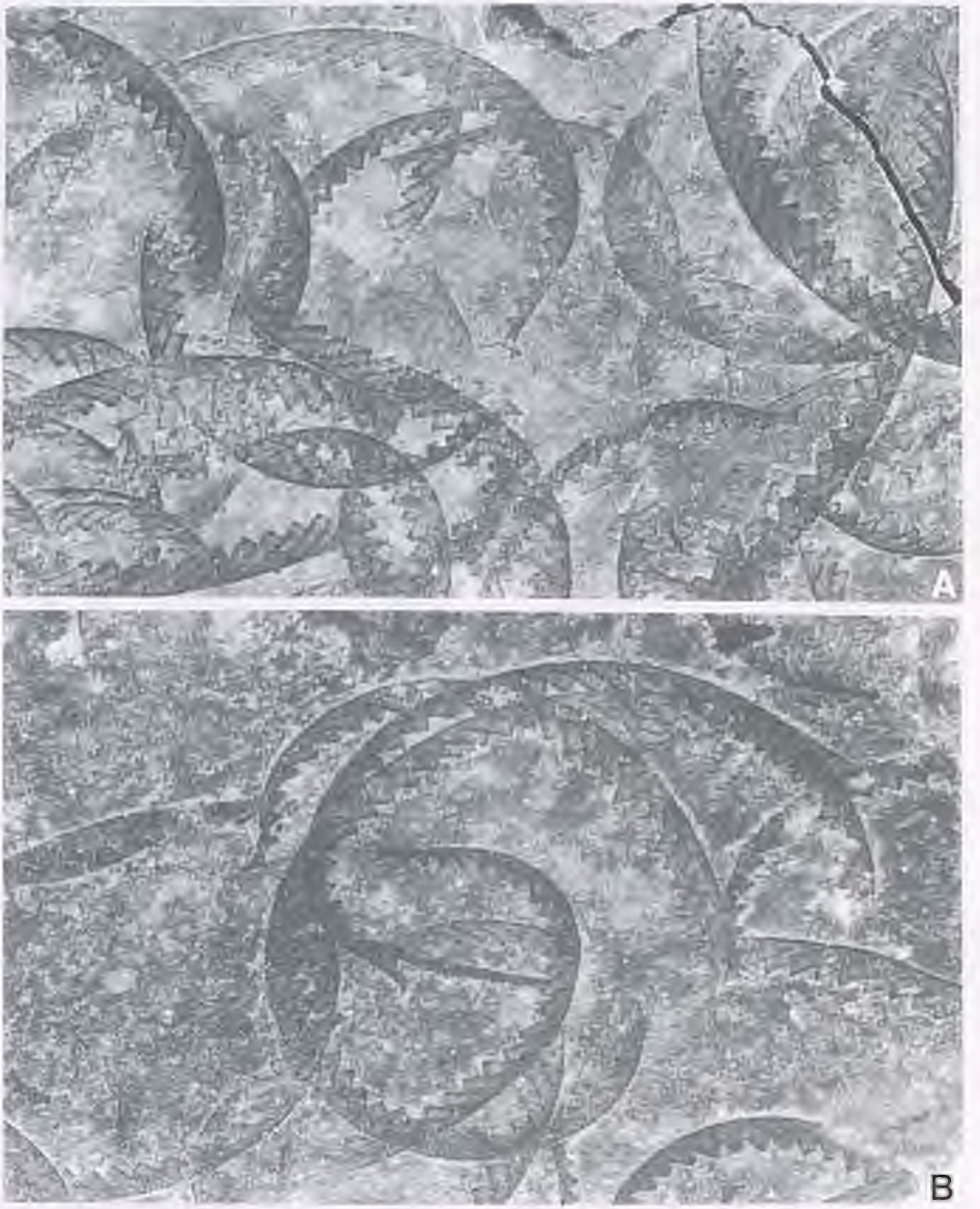

Figure 9. **A,B**, *Bohemograptus paracornutus* n.sp., W831, top of Black Bog Shale, *cornutus* Biozone: A—AMF 92364, B—AMF 92363. ×5.

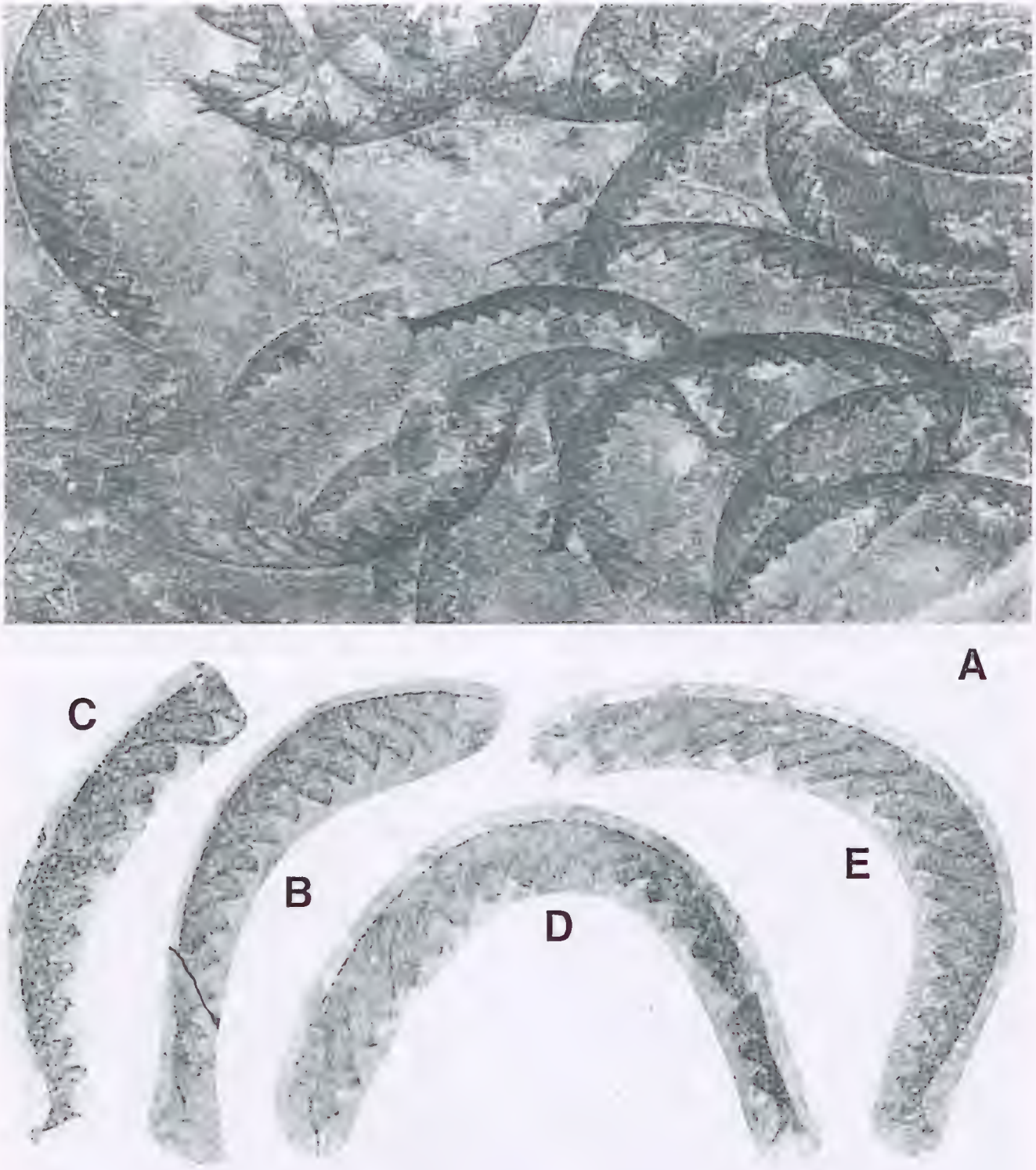

Figure 10. **A–E**, *Bohemograptus paracornutus* n.sp., top of Black Bog Shale, late Ludlow, Rainbow Hill, W831, *cornutus* Biozone, late Ludlow. A, slab AMF 92364, ×5; B, holotype AMF 92317, ×8; C–E, paratypes AMF 92322–24, all ×8.

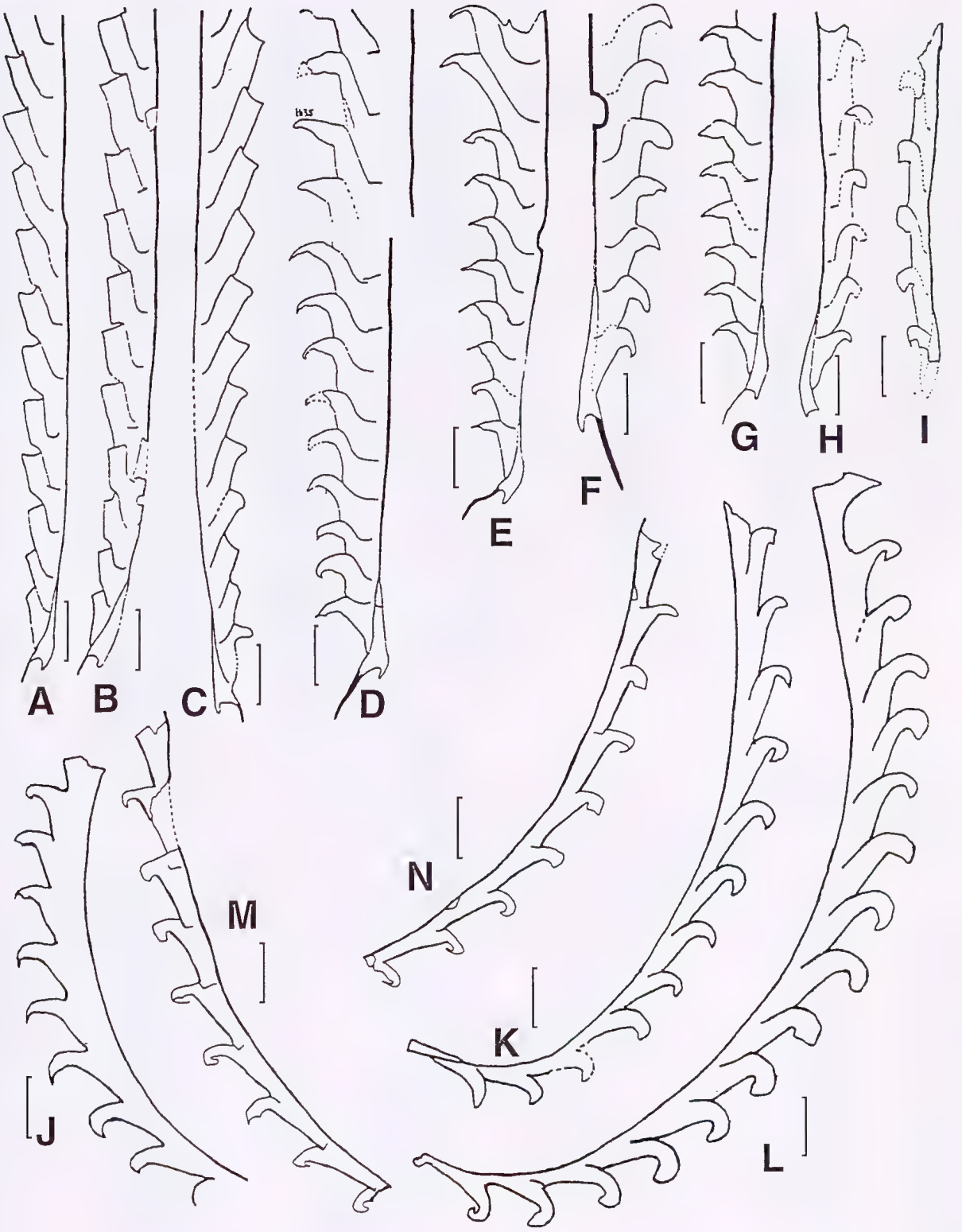

Figure 11. A–N, Graptolites from the Elmside Formation, *transgrediens* Biozone, Black Range Road, NW of Yass, W430. A,B, *Pristiograptus shearsbyi* n.sp., respectively AMF 102925, AMF 102926. C, *Monograptus transgrediens* Perner, 1899, AMF 102927a. D–G, *Monograptus hornyi* Jaeger (*in* Kříž *et al.*, 1986), respectively AMF 102920, AMF 102923, AMF 102924, AMF 102921. H,I, *Monograptus perneri elmsidensis* n.subsp., respectively holotype AMF 102922, and paratype AMF 103001. J–L, *Monograptus formosus formosus* Bouček, 1931b, respectively redrawn from Jaeger (1967, pl. 14b,c) and Packham (1968, pl. 11.4: AMF 71942, formerly SUP 23260), Derringullen Creek, Rosebank Shale, level 4 of Fig. 2. M,N, *Monograptus formosus jenkinsi* n.subsp., holotype ANU 35910, part and counterpart. Scale bars 1 mm.

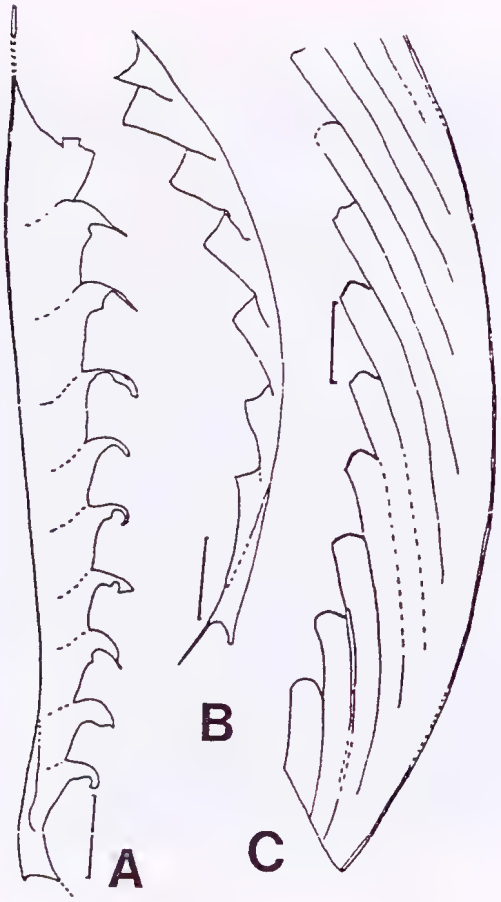

Figure 12. Selected Brown & Sherrard (1952) graptolites. **A**, *Monograptus bouceki* Přibyl, 1940, AMF 44608, Přídolí, Cowridge Siltstone, illustrated as *Monograptus salweyi* (Hopkinson, 1880) by Brown & Sherrard (1952, fig. 2b, pl. VIII, fig. b). **B**, *Bohemograptus b. tenuis* (Bouček, 1936), on same slab as Fig. 12C herein, AMF 44614, Ludlow, from Black Bog Shale (on same slab as *Egregiograptus* sp., but not figured by Brown & Sherrard, 1952). **C**, *Egregiograptus* sp., AMF 44614, Ludlow, Black Bog Shale; illustrated by Brown & Sherrard (1952, fig. 2f, pl. VIII, fig. g) as *Monograptus roemeri* (Barrande, 1850). Scale bars 1 mm.

COLLECTION LEVEL 1. The single specimen we record from our level 1, in the Yarwood Siltstone Member of the Black Bog Shale, is substantially higher stratigraphically than the records mentioned above. The occurrence of *Dictyonema* sp. cf. *D. sherrardae* Rickards *et al.*, 1995 at Yass is noteworthy, as it ranges in our collections from level 1 (Ludlow) up to level 4 (Přídolí). The species has previously been recorded as high as the *kozlowskii* Biozone in the Ludlow (Rickards & Wright, 1997) but not in the Přídolí.

COLLECTION LEVEL 2. Locality W830 at Rainbow Hill is where the upper part of the Black Bog Shale has yielded a rich assemblage, including the first record of *Bohemograptus praecornutus* Urbanek, 1970 in Australia.

In his preliminary comments on Yass graptolites from approximately this level, Jaeger (1967) distinguished "two subspecies of *M. bohemicus*", one a "lower subspecies ... the classical *M. bohemicus* subsp. A, which has rather simple thecae", and the other "with elaborated proximal thecae and sicula, is confined to the four metres immediately below the *Dalmanites* Bed", at our collection level 3. Jaeger's second form is almost certainly that described in this paper as *Bohemograptus paracornutus* n.sp. It is related to the *B. cornutus* lineages of Urbanek (1970) rather than to the *B. bohemicus* lineages *sensu stricto*. The exact nature of Jaeger's *B. b.* subsp. A is less certain; it may be the form which we describe below as *B. praecornutus* but, if so, its thecae are very similar to those of *B. paracornutus*. Alternatively, it may be that Jaeger identified *B. b. tenuis*, in which case his collection lacked *B. praecornutus*.

The stratigraphic significance is that *B. praecornutus* ranges, according to Urbanek (1970), through the eponymous biozone up into the succeeding *B. cornutus* biozone where it is less common. So locality W830, which yields *B. praecornutus* in abundance some 10–15 m below the *Dalmanites* Bed, is probably referable to the late Ludlow *praecornutus* Biozone, which is in agreement with our other data. Professor T. Koren′ (pers. comm.) has informed us that *praecornutus* ranges through the upper *scanicus, leintwardinensis* and *podoliensis* Biozones in central Asia.

COLLECTION LEVEL 3. Locality W831 at Rainbow Hill is in the top 2–3 m of the Black Bog Shale, and has yielded a small graptolite fauna (accompanied by sparse ceratiocarid debris, and occasional bivalves including *Cardiola* [Sherrard, 1960], ostracodes and small brachiopods) but nothing very distinctive except for the exceedingly abundant, complete, mature specimens of *B. paracornutus* n.sp. As a new species without any other known occurrences, it has no obvious stratigraphic value. However, we argue below, in the section dealing with evolution, that it derives directly from *B. praecornutus*; it is very likely, therefore, that it occurs at the *cornutus* Biozone level. *Bohemograptus cornutus* Urbanek, 1970 is, according to Urbanek (1970), itself a direct derivative of *B. praecornutus*. We have not found *B. cornutus* in the Yass sequence, nor has it been recorded previously from Australia; it is possible that *B. paracornutus* n.sp. and *B. cornutus* occupy different biogeographic provinces. It seems likely, then, that level three is approximately referable to the *cornutus* Biozone in global correlative terms. Presumably there is also a case, which we have not adopted here, for establishing a local *paracornutus* Biozone.

Figure 13 [continued from p. 209]. ... **E**, *Pristiograptus shearsbyi* n.sp., holotype AMF 92392, CowridgeSiltstone, Barambogie Creek, W834, Přídolí, ×10. **F**, *Pristiograptus kolednikensis* Přibyl, AMF 92353, W827, Rosebank Shale, Barambogie Creek, *parultimus* Biozone, Přídolí, ×10. **G**, *Monograptus hornyi* Jaeger, AMF 102923, Cowridge Siltsone, Barambogie Creek, W834, Přídolí, ×10. **H,I**, *Monograptus perneri elmsidensis* n.subsp., Elmside Formation, W430, Black Range Road, *transgrediens* Biozone, late Přídolí, both ×10; H, holotype AMF 102922; I, paratype AMF 103001. **J**, *Monograptus formosus jenkinsi* n.subsp., holotype ANU 35910, Elmside Formation, late Přídolí, Black Range Road, W430, *transgrediens* Biozone, late Přídolí, ×10. **K**, *Bohemograptus praecornutus* Urbanek, ×8, AMF 102898, Black Bog Shale, Rainbow Hill, W830, Late Ludlow, *praecornutus* Biozone, ×8. **L,M**, *Neocucullograptus? yassensis* n.sp., holotype AMF 92343, Rosebank Shale, Derringullen Creek, W828, *parultimus* Biozone, Přídolí, ×20, L, AMF 92343a; M, counterpart AMF 92343b.

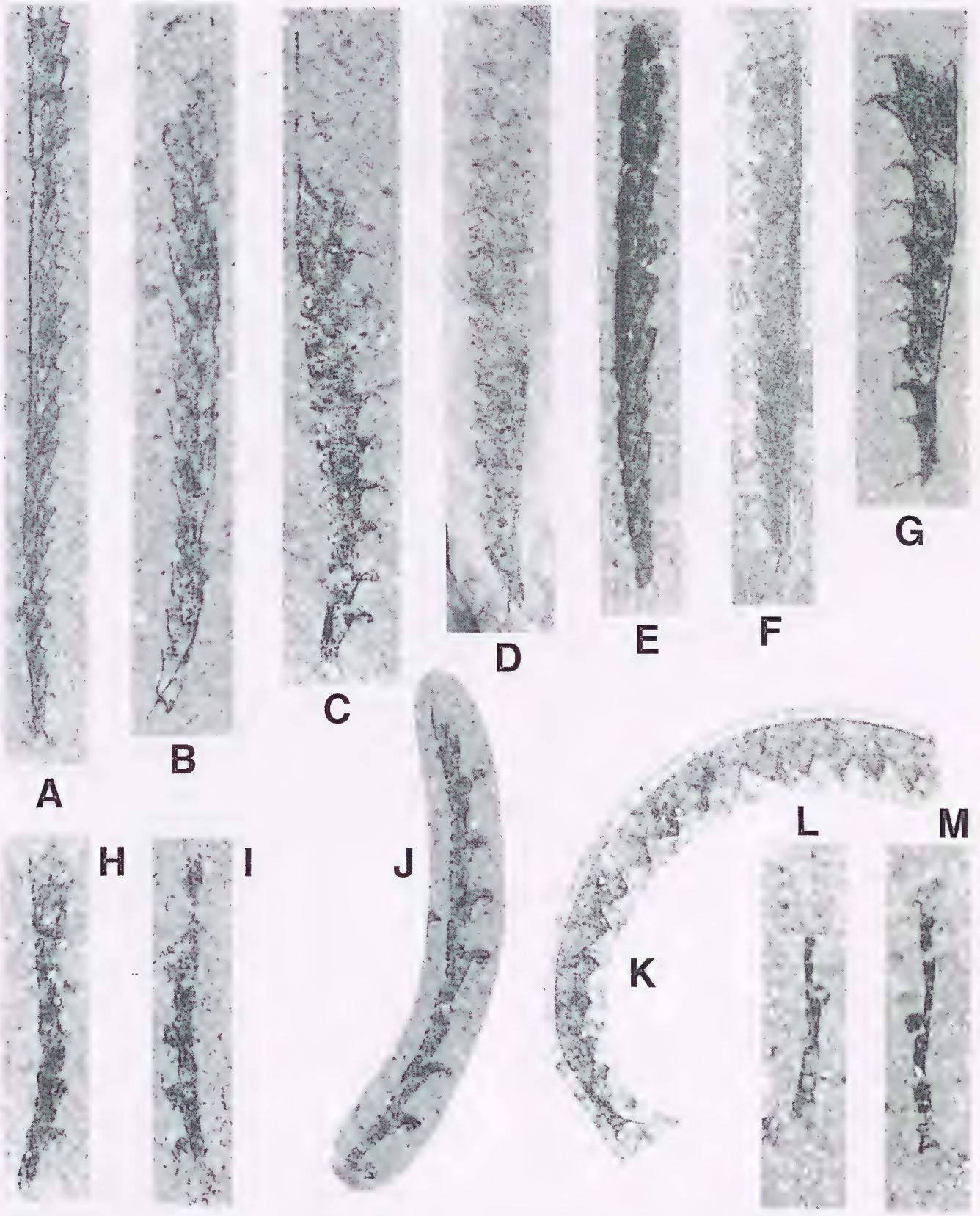

Figure 13. **A**, *Monograptus transgrediens* Perner. AMF 102927, Elmside Formation, Black Range Road, NW of Yass, W430, *transgrediens* Biozone, late Přídolí, ×5. **B**, *Pristiograptus shearsbyi* n.sp., paratype AMF 102925, Elmside Formation, Black Range Road, NW of Yass, W430, *transgrediens* Biozone, late Přídolí, ×10. **C**, *Monograptus bouceki* Přibyl, AMF 44608 (figured by Brown & Sherrard, 1952 as *Monograptus salweyi*), Cowridge Siltstone, Barambogie Creek, Přídolí, ×10. **D**, *Monograptus pridoliensis* Přibyl, AMF 92352, Rosebank Shale, W827, *parultimus* Biozone, Přídolí, ×10. ... [Caption continued on p. 208, opposite]

COLLECTION LEVEL 4. The next highest graptolite level, based on localities W171, W827 and W828, is unquestionably referable to the *parultimus* Biozone at the base of the Přídolí. The assemblage in the Rosebank Shale is quite rich, although several taxa occur a little higher than expected. The *parultimus* assemblage appears some 20 m above the base of the Rosebank Shale; thus the interval between collection level 3 (assigned above to the *cornutus* Biozone) and the *parultimus* Biozone is occupied by the Rainbow Hill Marl Member (formerly known as the Middle Trilobite Bed) and an overlying sequence of approximately 20 m of siltstone, shale and fine to medium sandstone. In terms of graptolite biozones this barren 20 m might be roughly the equivalent of the *inexspectatus* and *kozlowski* biozones, but it has yielded no graptolites to us (see Appendix 1 for a fuller discussion of the stratigraphic position of this level).

The base of the Přídolí is, therefore, located some 20 m above the base of the Rosebank Shale, and is marked by the incoming of a striking *parultimus* fauna. The fauna has some unusual features. Firstly, *Crinitograptus* Rickards, 1995 is recorded for the first time in the Přídolí; the species *C. operculatus* Münch, 1938 has been previously recorded from the late Ludlow of northwest mainland Europe. There are also two new minuscule graptolites which we questionably place in *Neocucullograptus* Urbanek, 1970 as *N.? yassensis* n.sp. and *N.? mitchelli* n.sp. The genus has not previously been recorded from the Přídolí and the two new forms are diminutive graptolites even by the standards of the genus.

COLLECTION LEVEL 5. One other locality, shown on Fig. 2 as W835, is the locality in the Rosebank Shale in Reedy Creek (see Fig. 1) from which Brown & Sherrard (1952) described a poorly preserved specimen as *M. vomerinus* (Nicholson); the only specimen we collected from this unlikely locality is ?*M. parultimus*.

COLLECTION LEVEL 6. Localities W832 and W833 are low in the Cowridge Siltstone at "Tulla Park" (Fig. 2) just N of the Good Hope Road. Details of the sparse fauna are given in the appendix; the fauna belongs, like level four, to the *parultimus* Biozone.

COLLECTION LEVEL 7. Locality W834 is in the Cowridge Siltstone in Barambogie Creek. Jaeger (1967) referred the latter level to the *bouceki* Biozone on the presence of the eponymous species, *M. bouceki*, and two forms of *M. transgrediens*. We comment in the Systematic palaeontology section on the latter species provisionally recognising, only *M. transgrediens transgrediens*. We concur with the *bouceki* Biozone attribution which leaves about 30 m of siltstones and sandstones, as yet barren of graptolites, which might be roughly equivalent to the (unproven) *ultimus* and *lochkovensis* biozones of other sequences in the world.

COLLECTION LEVEL 8. Locality W430, in the basal Elmside Formation on Black Range Road (Jenkins, 1982), is almost certainly referable to the latest Přídolí *transgrediens* Biozone. This is the conclusion reached by Jenkins (1982) who interpreted the early form *M.* cf. *angustidens* Přibyl, 1940 (typically low Devonian) as an evolutionary transient from *M. bouceki* to *M. uniformis angustidens*. We reidentify this form as *M. hornyi* Jaeger *in* Kříž *et al.* (1986), a typical Přídolí species. The presence of *M. transgrediens* also suggests a Přídolí age. The *perneri* Biozone, between *bouceki* and *transgrediens* has not been proved in this work, but there is some 50 m of siltstone and sandstone in between the two proven horizons. Jenkins (1982, p. 172) concluded that the base of the Devonian lies at about the middle of the Elmside Formation, between the (lower) sandy unit and the (overlying) shaley unit with limestone lenses yielding the diagnostic Lochkovian conodont *Icriodus woschmidti* (Fig. 2) as identified by Link & Druce (1972).

Biostratigraphy and evolution of the Yass graptolites

Dendroid graptolites. The rare, fragmentary dendroid rhabdosomes are quite well preserved, allowing observation of autothecal details of *Dictyonema* sp. cf. *D. sherrardae* and *D. elegans* Bulman, 1928. The former may be best regarded as the end member of a long-ranging species, first appearing in the *nilssoni* Biozone (Rickards *et al.*, 1995).

Dictyonema elegans is a very long-ranging species appearing in the late Wenlock of the UK; its range was extended into the *nilssoni* Biozone by Rickards *et al.* (1995), and then into the late Ludlow by Rickards & Wright (1997). The autothecal spacing changes up sequence (25 in the Wenlock and early Ludlow; 30 in the *praecornutus* and *cornutus* biozones; and 20 in the very latest Ludlow specimens). When more and better preserved material is available it seems likely that "*D. elegans*" will be divisible into several taxa.

Linograptids. *Linograptus posthumus introversus* Rickards & Wright, 1997 was first described from latest Ludlow strata near Wellington (N.S.W.), so the slightly earlier record herein from the *cornutus* level extends the range slightly; it has only been recorded elsewhere from Romania at about the same level (Rickards & Iordan, 1975). *Linograptus p. introversus* is best considered a short-lived, late Ludlow offshoot of the long-ranging (low Ludlow to Early Devonian), cosmopolitan *L. p. posthumus* (Richter, 1875) as both exhibit thecal introversion; it may prove to have some stratigraphic value. The only other endemic Australian form, the very early Ludlow (*nilssoni* Biozone) *L. orangensis* Rickards *et al.*, 1995 from the Quarry Creek area (N.S.W.), was transferred by Rickards & Wright (1997) to their new genus *Prolinograptus*. *Linograptus posthumus tenuis* Jaeger, 1959 from the Silurian (early Ludlow) *scanicus* Biozone of Thuringia differs in being a tiny form.

Bohemograptids. We have elsewhere (Rickards & Wright 1999) given an account of bohemograptid evolution in a fully global context; in summary, we recognise two main lines of evolution:

1. The *Bohemograptus bohemicus bohemicus* to *B. b. tenuis* line (of which we see late members in the Yass sequence at collection levels two and three); and
2. The *Bohemograptus cornutus* line (of which we record here *B. praecornutus* and its derivative *B. paracornutus*). The appearance of a trumpet-shaped sicula, as in *B. paracornutus*, is a feature seen in only a few lineages (e.g., *Saetograptus fritschi linearis* (Bouček, 1936) and *Monograptus deubeli* Jaeger, 1959) below the Devonian (where, typically, it appears in the *hercynicus* and related lines), and never to the bizarre extent as in *B. paracornutus*.

Pristiograptids. Jaeger (1967, p. 282) noted that "morphologically advanced forms of the long-ranging group of *M. dubius* have been found". However, in the absence of figures, descriptions or specimens (see previous comments about Jaeger's Australian collections) it is difficult to know to what he was referring. From W830 at Rainbow Hill (i.e. *praecornutus* Biozone) we have obtained *Pristiograptus dubius* (Suess, 1851) itself, which is known to range into the Přídolí (see Koren′ & Sujarkova, 1997). We illustrate the form as Figs. 3G–I and note, in our description below, that the sicula has a pronounced dorsal tongue, much more so than in earlier Ludlow forms. It may be this form to which Jaeger referred. However, in the same beds, but more long-ranging overall at Yass (Fig. 2) is *P. shearsbyi* n.sp., a much more slender species than *P. dubius*, but also possessing a (short) dorsal sicular tongue. Jaeger (1967) did not refer to this form and may well have missed it on Barambogie Creek, where it is common and whence he recorded *M. bouceki* and *M. transgrediens*. It seems likely that *P. shearsbyi* is a gracile offshoot of the stem lineage of *P. dubius*; such slender species (as well as broad species) were derived repeatedly from the *P. dubius* lineage from the low Wenlock to the latest Ludlow (Rickards *et al.*, 1977, fig. 31), and most were short-lived species rarely lasting more than a couple of zones. By comparison (Fig. 2) *P. shearsbyi* was rather long-lived for such a form, ranging from the *praecornutus* zone (late Ludlow) to the *transgrediens* zone (late Přídolí).

Pristiograptus kolednikensis Přibyl, 1940 is here distinguished from the late Ludlow *P. fragmentalis* (Bouček, 1936) largely because it is less robust (maximum width 2 mm) and has a lower Σ value. *Pristiograptus fragmentalis* is much more commonly recorded, globally speaking, and our specimens do resemble *P. fragmentalis* as illustrated by Koren′ & Sujarkova (1997). The Yass material is, however, noticeably narrower and fits Přibyl's description of *P. kolednikensis* well. Both species must be related to *P. dubius*, but the proximal ends of both are straighter and the earlier thecae are inclined to the rhabdosomal axis at a higher angle. They are best considered late, robust offshoots of the stem lineage of *P. dubius*. The exact horizon of *P. kolednikensis* in Europe is in some doubt, but at Yass it occurs in the *parultimus* Biozone, which is above the range of *P. fragmentalis*. It is thus tempting to suggest that the Přídolí *P. kolednikensis* is a late derivative of *P. fragmentalis* rather than a direct offshoot of *P. dubius*; both differ from *dubius* in their high angle of inclination of th 1 (40–45°), whereas in *dubius* the angle is 20–30°.

Monograptids. *Monograptus pridoliensis* Přibyl, 1981. The evolutionary setting of this species was last discussed by Rickards & Garratt (1990). They supported Koren′'s (1983) proposition that a likely lineage was of *M. pridoliensis* → *M. prognatus* (both Přídolí) → *M. uniformis angustidens* (early Devonian). As Jenkins (1982) and Rickards & Garratt (1990) have shown, *M. uniformis*-like forms do occur in the late Přídolí (respectively *M.* cf. *angustidens* and *M. u.* cf. *parangustidens*). The stratigraphic occurrences of these species, and their morphological features suggest an evolutionary lineage as follows: *M. pridoliensis* (=*M. similis* Přibyl, 1940) in the early Přídolí; leading to *M. prognatus* and *M. bouceki* in the mid-Přídolí; and thence to early morphotypes of *M. uniformis* in the latest Přídolí. The changes involved are relatively subtle and include less biformity of the thecal hoods in the latest forms and an increase in the Σ values as the proximal end becomes more robust (Koren′, 1983).

Monograptus perneri elmsidensis n.subsp. is close to but narrower than the type subspecies and *M. p. kasachstanensis* Mikhajlova, 1975: in view of its occurrence in the latest Přídolí *transgrediens* Biozone, it seems best to regard it as a very late, rare form derived from *M. p. perneri* (*perneri* Biozone, late Přídolí) which it resembles in general rhabdosomal form. *Monograptus formosus jenkinsi* n.subsp., again from the latest Přídolí *transgrediens* Biozone, may well be a late derivative of *M. f. formosus* which occurs in the *parultimus* Biozone at Yass and ranges from late Ludlow to early Přídolí in Europe (Jaeger, in Kříž *et al.*, 1986).

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Appendix

Locality data for Yass localities cited

All collection sites (Fig. 1) are located on the Yass 1: 50 000 topographic sheet (8628-S), and all grid references (GR) refer to that sheet. With the exception of the first three localities below which were made earlier by AJW, all collections were made by the authors in December 1997.

W69 Black Bog Shale, Yarwood Siltstone Member (= "Lower Trilobite Bed" of Brown, 1941); Derringullen Creek, GR 713477. Ludlow. Apart from dendroids reported by Jaeger (1967) from low in the Black Bog Shale, and graptolites possibly from this horizon (Shearsby, 1912), this is the lowest known Ludlow graptolite from Yass. *Dictyonema* sp. cf. *D. sherrardae*; collected by AJW in 1972.

W171 Collected by AJW in 1974. GR 715472. This is probably the locality of Packham (1968) and Jaeger (1967) at the crossing of the highway and Derringullen Creek. The small quarry, probably that shown by Link & Druce (1972), was largely destroyed during the construction of the dual carriageway in the early 1970s. It appears to be very close stratigraphically to W827 and W828 (see below). The fauna is early Přídolí, belonging to the *parultimus* Biozone.

The locality lies perhaps as much as 30 m above the base of the Rosebank Shale. Because the Rainbow Hill Marl does not outcrop in this vicinity, the stratigraphic interval separating the Marl from the overlying fossiliferous level is uncertain. It was said by Packham (1968) to be "within a hundred feet" and a label accompanying a specimen in the Australian Museum and written by I.A. Browne states that the interval is as little as 20 ft (ca. 6 m); Jaeger (1967) stated that these beds yielding our *parultimus* fauna "have a maximum thickness of 30 m and immediately overlie the *Dalmanites* Bed" (i.e., the Rainbow Hill Marl Member). The collective fauna from this locality, W827 and W828, as well as taxa recorded by Packham and Jaeger, is: *Dictyonema* sp. cf. *D. sherrardae*; *Dictyonema* sp.; "*Medusaegraptus*" sp.; *Monograptus parultimus* Jaeger, 1975; *M. pridoliensis* Přibyl, 1981; *Monograptus formosus formosus* Bouček, 1931b; *Crinitograptus operculatus* (Münch, 1938); *Neocucullograptus? mitchelli* n.sp.; *Neocucullograptus? yassensis* n.sp.; *Linograptus posthumus posthumus* Richter, 1875; *Pristiograptus kolednikensis* Přibyl, 1940; and *Pristiograptus shearsbyi* n.sp. No associated fauna has been recorded from these localities, although possible plant fragments were noted.

W430 Black Range Road cutting in the lower part of the Elmside Formation (Jenkins, 1982); GR 696447. The sequence consists of alternating shale and fine micaceous sandstone beds; the latter have been the source of all our graptolites and commonly show HCS and shallow water sole markings. Associated fauna (see also Link & Druce, 1972) includes most commonly the brachiopod *Plectodonta bipartita* Chapman (normally cited as a senior synonym of

Plectodonta davidi Brown) occurring as abundant disarticulated, disoriented valves, and *Lissatrypa*; and rare trilobites such as *Kettneraspis rattei* (Etheridge & Mitchell). Large (up to ca. 10 mm) amorphous carbonaceous bodies also occur with the graptolites. The low diversity but well-preserved and abundant graptolite fauna is dominated by *Linograptus posthumus posthumus* and the monograptids: *Monograptus transgrediens* Perner, 1899; *Monograptus hornyi* Jaeger (*in* Kříž *et al.*, 1986); *Monograptus perneri elmsidensis* n.subsp., a single specimen of *Monograptus formosus jenkinsi* n.subsp., and the dendroid *Dictyonema elegans* Bulman, 1928. This fauna is late Přídolí. First AJW collections made in 1982.

W827 Low bare shale outcrops on W bank of Derringullen Creek, upstream of motorway bridge. GR as for W171. This locality has yielded the *M. parultimus* fauna, which is listed in its entirety under W171. We have not collected *M. formosus* at this locality, nor at W828.

W828 This locality is about 15 m further W from W827 but has similarly been grouped with W171. GR as for W171 and W827.

W830 Rainbow Hill, about 15 m below the top of the Black Bog Shale; GR 712409; *praecornutus* Biozone, late Ludlow. Fauna includes: *Monograptus bohemicus tenuis* Bouček, 1936; *Monograptus praecornutus* Urbanek, 1970; *Pristiograptus shearsbyi* n.sp.; *Pristiograptus dubius* Suess, 1851; *Linograptus p. posthumus*; *Dendrograptus* sp.; and *Dictyonema elegans* Bulman, 1928.

W831 Rainbow Hill, uppermost 2–3 m of the Black Bog Shale; GR 712409. The fossiliferous strata are layered organic-rich shales with abundant pyrite on bedding planes, although the graptolites are not pyritised. Bedding planes are often covered with overlapping, complete, mature rhabdosomes. The associated very sparse fauna includes: the rare clams (Sherrard, 1960) *Cardiola, Pteronitella rugosa* Sherrard, 1960, *Actinopterella minuta* Sherrard, 1960; and rare small brachiopods, ceratiocarids, ostracodes, nautiloids and trilobite elements. The gradational contact with the shallow water marls of the Rainbow Hill Marl Member of the Rosebank Shale indicates a marked regression. Slight tectonic deformation has produced the normal different appearances of the fossils in the two extreme conditions. The graptolite fauna includes: *Dictyonema elegans*; *Dictyonema* sp. cf. *D. sherrardae*; *Linograptus posthumus posthumus*; *Linograptus posthumus introversus* Rickards & Wright, 1997; *Monograptus paracornutus* n.sp.; and *Monograptus bohemicus tenuis*. Contrary to the statement by Brown & Sherrard (1952), this *bohemicus* fauna was first found by Dr Gordon Packham in 1947 at Rainbow Hill and subsequently material was made available to Dr Ida Brown and Mr A.J. Shearsby (Gordon Packham, pers. comm., 1998). Note that there is some further confusion in locality data given by Brown & Sherrard (1952, p. 130).

W832, W833 Cowridge Siltstone, "Tulla Park", mostly from fine sandstone rubble low in formation, on low ridge west of farm track; GR 724385. The former locality is in the northern part of portion 15, the latter in the southern. This is presumably the "*salweyi*" horizon of Brown & Sherrard (1952, fig. 1). Fauna consists of: *Monograptus parultimus* Jaeger, 1975 and *Pristiograptus shearsbyi* n.sp. As indicated by Jaeger (1967) no monograptids with hooked thecae were found here.

W834 Cowridge Siltstone, Barambogie Creek, GR 693515; all material from float, but apparently derived from no lower than halfway up lower unit recognised by Link & Druce (1972). This locality is close to the "Silverdale" locality of Sherrard & Keble (1937) which was from a ridgetop (portion 34, parish of Derringullen) just N of the creek near the Yass-Boorowa road (Fig. 1). The photograph published by Brown & Sherrard (1952), purporting to be of this Silverdale locality, is a view of Rainbow Hill from the North. Fauna includes: *Dictyonema* sp., *Monograptus transgrediens, M.* sp., *M. bouceki* and *Pristiograptus shearsbyi*.

W835 Rosebank Shale, Reedy Creek. Collecting at this roadside locality was undertaken because Brown & Sherrard (1952) described material from (presumably) here as *Monograptus vomerinus* (Nicholson); our only poor material is a very doubtful *Monograptus parultimus*. GR 698372.